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Ecological Studies of the TIMBER WOLF in Northeastern Minnesota

NORTH CENTRAL FOREST EXPERIMENT STATION
FOREST SERVICE
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FOREWORD

The largest population of timber wolves remaining in the United States (excluding Alaska) lives in northern Minnesota. Many of these wolves inhabit the Superior National Forest, so protecting the habitat of this endangered species is largely a Forest Service responsibility.

As the "Age of Ecology" broadens into the 1970's, wolves and wolf habitat will become a subject of concerted research. Forest land managers will have to know more about how the timber wolf fits into a forest system. Building on nearly 50 years of research in northern forests, we at the North Central Station intend to expand our studies of wildlife habitat. We are happy to publish the enclosed papers as one step in this direction.

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ECOLOGICAL STUDIES OF THE TIMBER WOLF IN NORTHEASTERN MINNESOTA

L. David Mech and L. D. Frenzel, Jr. (Editors)

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MOVEMENTS, BEHAVIOR, AND ECOLOGY OF TIMBER WOLVES IN NORTHEASTERN MINNESOTA

L. David Mech, L. D. Frenzel, Jr.,
Robert R. Ream, and John W. Winship

The largest population of wolves (*Canis lupus*) remaining today in the continental United States outside of Alaska is in northern Minnesota. As of mid-1970 this population was not legally protected, and the species, which once ranged over almost all of North America, is now considered by the U.S. Department of the Interior to be in danger of extinction in the contiguous 48 States. Until the present research, the only field studies of Minnesota wolves were those of Olson (1938 a, b) and Stenlund (1955). Those investigations provided much useful general information about Minnesota wolves and gave the present authors an excellent background with which to begin more detailed investigations.

This paper reports on the basic aspects of a series of studies that began in 1964, and concentrates primarily on wolf movements and activity, social behavior, hunting behavior, and population organization. Most of the data were collected during January, February, and March 1967; February, November, and December 1968; and January through August 1969. A total of 192 days was spent in the field.

According to a distribution map of wolf subspecies (Goldman 1944), the race of wolves in our study area is *Canis lupus lycaon*. However, evidence presented by Mech and Frenzel (see page 60) suggests that there may be strong influence by *C. l. nubilus*, a more western race of wolf formerly thought to be extinct (Goldman 1944).

Between 1965 and the present, wolves in the study area were neither protected nor bountied, and the influence of trapping and hunting is thought to have been negligible.

THE STUDY AREA

This study was conducted in the Superior National Forest (fig. 1) in northern St. Louis, Lake, and Cook Counties of northeastern Minnesota (92° west longitude, 48° north latitude), an area well described by Stenlund (1955). Most of the data were collected from within and immediately south of the Boundary Waters Canoe Area, a special wilderness region in which travel by motorized vehicles is restricted. The total study area encompasses approximately 1.5 million acres, and numerous lakes and rivers comprise about 15 percent of this area (fig. 2). The topography varies from large stretches of swamps to rocky ridges, with altitudes ranging from 1,000 to 2,300 feet above sea level (fig. 3). Winter temperatures lower than -30° F. are not unusual, and snow depths generally range from 20 to 30 inches on the level. However, an important exception occurred in early 1969 when depths of 45 inches and more accumulated in much of the area. Further details on snow conditions in the study area during the period of this investigation are given by Mech *et al.* (see page 51). Conifers predominate in the forest overstory, with the following species present: jack pine (*Pinus banksiana* Lamb.), white pine (*P. strobus* L.), red pine (*P. resinosa* Ait.), black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*P. glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), white cedar (*Thuja occidentalis* L.), and tamarack (*Larix laricina* (DuRoi) K. Koch). However, as a result of extensive cutting and fires much of the conifer cover is interspersed with large stands of white birch (*Betula papyrifera* Marsh.) and aspen (*Populus tremuloides* Michx.). Detailed descriptions of the forest vegetation were presented by Ohmann and Ream (1969).

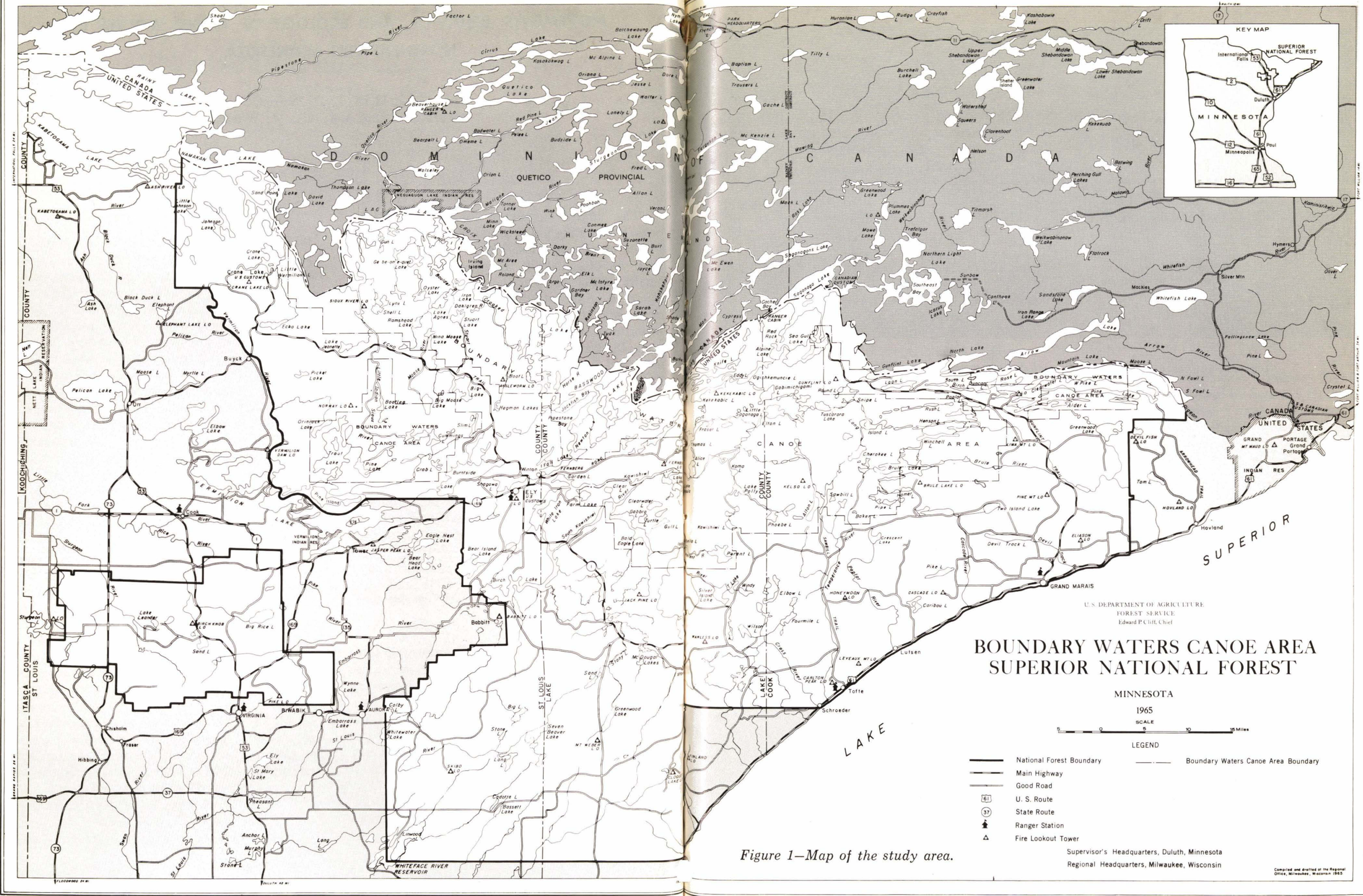

Figure 1—Map of the study area.

Figure 2.—Lakes are common throughout most of the study area. (Photo courtesy of L. D. Mech.)

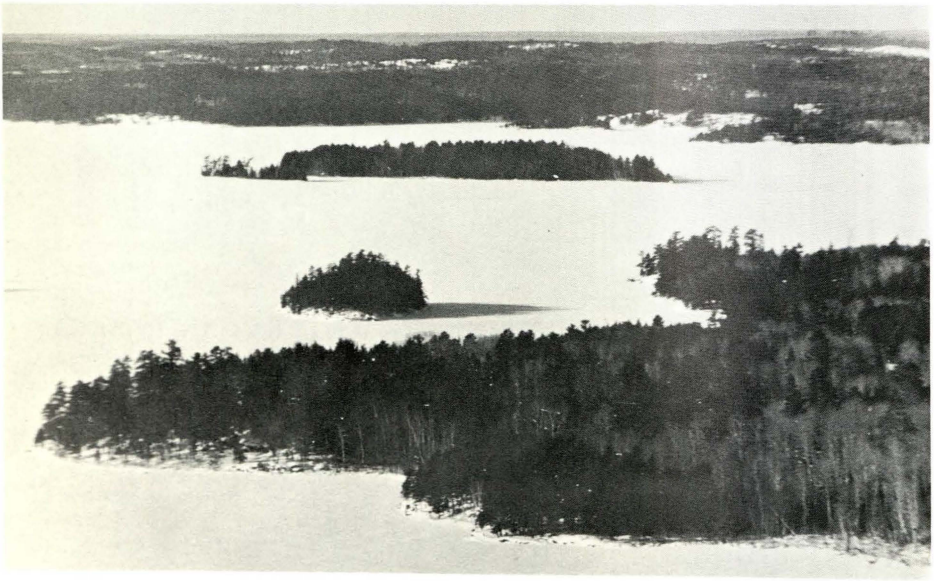

Figure 3.—Ridges, islands, swamps, and bays are part of the variable topography in the Superior National Forest. (Photo courtesy of L. D. Mech.)

METHODS

The observations discussed in this paper were all made from aircraft, the method of flying being that reported by Burkholder (1959) and Mech (1966a). The following aircraft were used (in order of size): Aeronca Champ,[1] Supercub, Cessna 172, Cessna 180, and Cessna 206. The smaller aircraft were excellent for holding in tight circles during observations but had the disadvantage of being slow and cold; the larger planes could cover the study area much more quickly and were more comfortable, but were not as maneuverable during observations. For radiotracking, to be discussed below, the best compromise seemed to be a Cessna 172.

To make observations of wolves, we flew over frozen waterways until tracks were found, and then followed the tracks until we lost them or saw the wolves (fig. 4). Several times we located wolves directly just by scanning the lakes. However, because there seemed to be a number of packs in the area, and because most wolves were the same color (with the exception of a few black or white individuals (see Mech and Frenzel, page 60), it usually was not possible to follow packs from one day to the next and be certain of identification. Moreover, it was impossible to locate any pack at will because most wolves also spent much time inland.

Therefore, to facilitate our observations and to obtain data on wolf movements and extent of range, we began a radiotracking program in 1968-69. A professional trapper, Robert Himes, was employed to capture the wolves. Using Newhouse No. 4 and 14 steel traps at scent-post sets, he caught two wolves, and captured another with a live-snare similar to that used by Nellis (1968); the senior author trapped two additional wolves (fig. 5).

The four wolves held in steel traps were restrained by a choker (fig. 6), and then anesthetized by intramuscular injections (fig. 7A, B) of a combination of 30 mg. of phencyclidine hydrochloride (Sernylan, Parke-Davis Co.) and 25 mg. promazine hydrochloride (Sparine, Wyeth Laboratories) as prescribed by Seal and Erickson (1969); these drugs proved most satisfactory.

The fifth wolf (a female), which was captured around the chest by the live-snare, was handled without drugs. A forked stick was used to hold down her head (Kolenosky and Johnston

[1] *Mention of trade names does not constitute endorsement by the USDA Forest Service.*

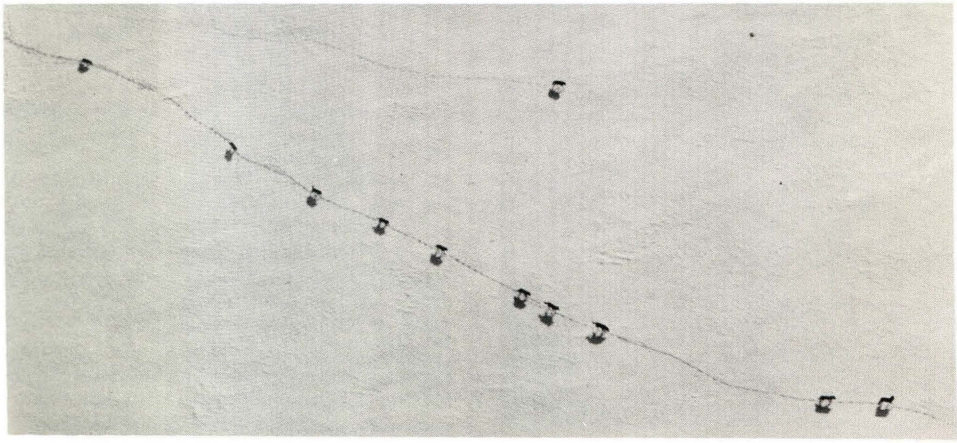

Figure 4.—An important technique used in the study involved aerial tracking and observing of wolf packs. (Photo courtesy of L. D. Frenzel.)

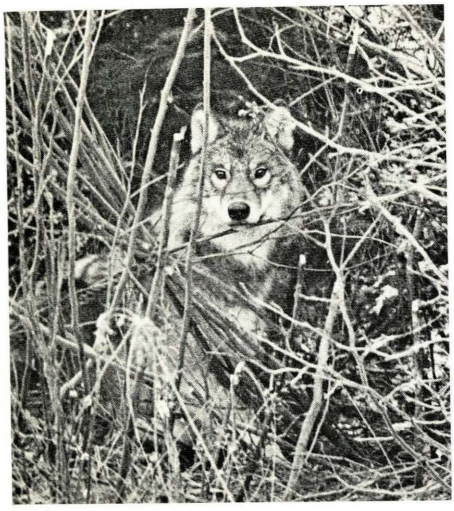

Figure 5.—A wolf caught in a trap. (Photo courtesy of D. L. Breneman.)

Figure 6.—A choker was used to restrain wolves caught in traps. (Photo courtesy of D. L. Breneman.)

Figure 7.—A. A small hypodermic syringe is loaded with drugs. B. The loaded syringe is used on the end of a pole. (Photos courtesy of D. L. Breneman.)

1967), and she offered no resistance (fig. 8). Evidently she went into shock or some other psychophysiological state of unconsciousness, for after her release she remained on her side and did not move for 1.5 hours, despite our prodding during the first few minutes (fig. 9). Then suddenly she leaped up and ran off.

Each wolf was examined, outfitted with a radio transmitter collar 15 inches inside circumference (fig. 10) and tagged with identification numbers in both ears (fig. 11). Each transmitter was of a different frequency in the 150 MH_Z range, emitted a pulsed signal ranging from 75 to 350 pulses per minute, and had a calculated

Figure 8.—Once pinned by the forked stick, the wolf ceased struggling. (Photo courtesy of Richard Bend.)

Figure 10.—A radio transmitter collar was placed around the neck of each trapped wolf. (Photo courtesy of D. L. Breneman.)

Figure 9—After release, the wolf lay still for 1½ hours before jumping up and running off. (Photo courtesy of L. D. Mech.)

Figure 11.—Each ear of the wolf was tagged with identifying numbers. (Photo courtesy of Richard Bend.)

life of at least 300 days (fig. 12). Two types of 12-inch whip antennas were used on the transmitters: one type extended up the side of the collar and then stuck out above for 6 inches; the other was fully attached inside the collar and extended up one side, around the top, and partly down the other side. The transmitter, batteries, and antenna were molded into a collar of acrylic weighing 11 ounces (Mech *et al.* 1965).[2] All radio equipment functioned flawlessly for at least 5 months, and one transmitter continued operating for at least 9 months.

Figure 12.—Each radio collar had a different frequency tuned to special receivers, which allowed each wolf to be identified. (Photo courtesy of D. L. Breneman.)

For tracking radio-equipped wolves, a directional yagi antenna (fig. 13) was attached to each of the wing struts of an aircraft and connected inside to a portable receiver. The usual tracking technique was to fly at 1,500 to 3,000 feet elevation to the last known location of the wolf being sought (fig. 14). If a signal was not obtained at that point, the aircraft spiraled upward until the signal was found or until 10,000 feet altitude had been reached. If the signal still was not heard, a search pattern was flown at 10,000 feet. The range of the signal from this altitude was 15 to 35 miles; at 3,000 feet it was 10 to 15 miles. Collars with antennas molded fully inside gave only about two-thirds the range of those protruding partly, but could be expected to last longer because the antennas could not break off. It is unknown whether any protruding antennas did break during the study, but on January 5, 1970, one wolf was recaptured, and its antenna had broken.

Figure 13.—Directional yagi antennas fastened to the wing struts of the aircraft were necessary to "home in" on the wolves. (Photo courtesy of U.S. Bureau of Sport Fisheries and Wildlife.)

Figure 14.—The tracking aircraft was usually flown at altitudes of 1,500 to 3,000 feet. (Photo courtesy of Dick Shank.)

[2] *The acrylic collar was fashioned by the Davidson Co., Minneapolis, Minnesota, which also produced some of the transmitters. Other transmitters and two radio receivers were manufactured by the AVM Instrument Co., Champaign, Illinois.*

When a signal was received, the aircraft was headed in the approximate direction of the source until the signal strength reached a peak; a 90° turn was then made in the direction the signal seemed the strongest. A series of these maneuvers soon narrowed the area to the point where visual search was possible. After practice and experience with this technique, we could locate the approximate source of the signal within 10 to 30 minutes after first receiving it.

Even though the radiotagged wolves spent most of their time inland, often in stands of conifers, they were frequently observed from the aircraft. The technique was to circle at 300 to 800 feet altitude around a radius of a quarter mile from the point where the strongest signal emanated. From December through April, 65 percent of the wolves located by radio were sighted; the rate was much higher for more experienced personnel. A pack of five wolves that was tracked was seen 31 times out of 33 attempts during February and March.

Whenever wolves were located, radiotagged or not, observations were made from an altitude that did not disturb them. Packs varied in the concern shown the aircraft, but only one or two ran from it. The radiotagged wolves, and a pack of 10 to 13 animals, were habituated to the aircraft and usually could be observed from altitudes of 500 feet and less without disturbance (fig. 15).

Almost all the radiotracking was done from aircraft, but when inclement weather prevented flying, some attempts from the ground succeeded when wolves were close enough to roads. The usual range on the ground was 0.75 to 1.50 miles. One wolf was approached to within 35 feet through radiotracking.

RESULTS AND OBSERVATIONS

Aerial observations made during this study involved 490 hours distributed as follows: January, February, March 1967 — 124 hours; February 1968 — 10 hours; December 1968 through August 1969 — 356 hours. Seventy-seven observations involving a total of 323 wolves were made (table 1), excluding animals located through radiotracking.

One male and four female wolves were radiotagged, and they and their associates were followed intermittently for periods of 5 to 8 months (table 2). All except one initially suffered some injury to a foot. Three of these animals were

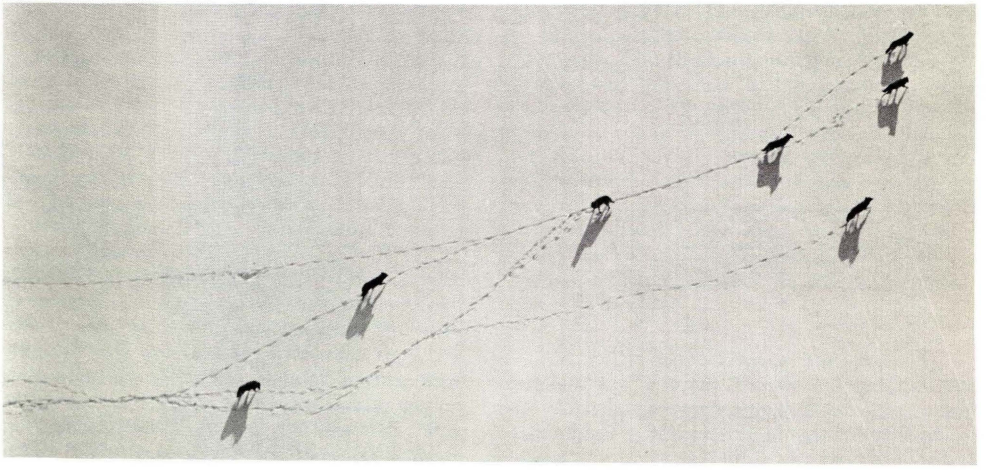

Figure 15.—The wolves studied soon became accustomed to the aircraft and could then be observed during their natural activity. (Photo courtesy of L. D. Mech.)

Table 1.—Sizes of wolf population units observed in northeastern Minnesota

Population unit[1] (number of wolves)	Wolf observations							
	Winter 1966-67		Winter 1968-69		Total		Winters[2] 1948-53	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
1	8	31	17	33	25	32	48	43
2	3	12	6	12	9	12	24	22
3	3	12	2	4	5	6	7	6
4	--	--	7	14	7	9	7	6
5	2	7	4	8	6	8	8	7
6	3	12	4	8	7	9	7	6
7	2	7	1	2	3	4	4	4
8	3	12	3	6	6	8	3	3
9	--	--	2	4	2	3	3	3
10	2	7	2	4	4	5	--	--
11	--	--	--	--	--	--	--	--
12	--	--	1	2	1	1	1	1
13	--	--	2	4	2	3	--	--
Total number of wolves	109	--	214	--	323	--	318	--
Total number of observations	26	--	51	--	77	--	112	--
Mean population unit size	4.2	--	4.2	--	4.2	--	2.8	--

1/ Because wolf packs sometimes split temporarily, these figures may not strictly represent actual pack sizes; nevertheless they should provide reasonably accurate approximations.
2/ From Stenlund (1955).

Table 2.—Background information on five radiotagged wolves studied in northeastern Minnesota

Wolf		Estimated weight[1] (pounds)	Usual associations	Location captured	Date captured	Last date located	Days located	General condition
Number	Sex						Number	
1051	M	75	None[2]	T62N-R7W-S18	Nov. 27/68	Apr. 24/69	84	Good, but two toes frozen in trap; animal limped lightly for 5-6 wks.
1053	F	60	None	T62N-R8W-S13	Dec. 10/68	Aug. 29/69	72	Thin; top of foot cut in trap but no broken bones or frozen toes; limped for at least 10 wks.
1055	F	60	Another wolf intermittently	T61N-R10W-S26	Jan. 5/69	May 30/69	65	Thin; two toes lightly frozen; no limp ever noticed.
1057	F	60	Pack of 13[3]	T66N-R5W-S33	Jan. 8/69	Apr. 24/69	47	Thin; front foot frozen in trap; lost use of foot and could not stay with pack.
1059	F	65	Pack of 5	T62N-R11W-S26	Jan. 22/69	Aug. 29/69	51	Good but thin; captured in snare; no apparent injury.

1/ Wolf 1059, when killed by a trapper on January 10, 1970, appeared to be of the same size and condition as when radiotagged; she only weighed 53 pounds, however, indicating that probably all the weights are overestimated.
2/ Tracks of a pack of at least two other wolves came by trap where 1051 was caught; however, there was never any other indication that 1051 may have been a member of a pack.
3/ A frozen foot prevented 1057 from staying with her pack; but she did associate with other wolves intermittently and with the whole pack when it came by her restricted area.

seen limping, but only in one case was the limp judged extreme enough to have significantly affected the movements or behavior of the animal. In that one case, the wolf (No. 1057) was caught in a steel trap on an extremely cold night, and her foot froze. After that she was often seen hopping on three legs. She was not able to keep up with her pack, which consisted of 10 to 13 members, and her movements were much restricted compared with those of other wolves. However, she was frequently observed feeding on fresh kills, and may even have made them herself.

The precise ages of the radiotagged wolves were unknown. All individuals, however, had sharp unworn teeth, indicating that they were

all relatively young. No. 1051, the only male studied, had testes 2.0 cm. long and 1.5 cm. wide; their volume therefore would be less than 4.5 cc. The small size of these testes, compared with the 7 to 28 cc. reported by Fuller and Novakowski (1955) as the volume of the testes from wolves taken during fall, would indicate that 1051 had not yet matured. Since the animal's testes and canine lengths were considerably greater than those of pups caught in a later study, we presume 1051 was 18 or 30 months old.

Two of the females, No. 1055 and No. 1059, both captured in January, had vulvas that seemed to be beginning to swell. No. 1059 was killed by a trapper about a year later, on January 10, 1970, and an examination revealed that she had bred in 1969 and carried five fetuses. Sectioning her incisors and reading the apparent annulations indicated that she probably was 3+ or 4+ years old.[3]

Three of the wolves were basically lone individuals. One of these, No. 1051, was captured on a night when tracks of at least two other wolves came by the trap, and this could mean that he had been part of a pack. However, it is also possible that these were merely tracks of non-associated wolves that were also traveling through the area. In any case, 1051 was not seen associating with any other wolf until 4 months after he was caught, and even then the association seemed to be temporary and casual. It could be argued that capture, handling by humans, or wearing a collar prevented him from regaining old associations or making new ones. However, the wolves radiotagged by Kolenosky and Johnston (1967) were quickly accepted back into their packs, and so were two of ours. Thus we conclude that 1051 probably was a lone wolf when captured.

When 1053 was trapped, her tracks were the only ones in the area, and she was never seen closely associating with another wolf. No. 1055 probably was with another wolf when captured, as evidenced by tracks. About a month after she was radiotagged she associated with another wolf intermittently for about 2 weeks, after which she was only seen alone.

[3] *David W. Kuehn. Personal correspondence to L. D. Mech, 1970.*

No. 1057 and No. 1059 were both members of packs. No. 1057 was captured during the night after a pack of 13 wolves was seen heading toward the area; 5 days later she was seen with 10 other wolves, which no doubt represented this same pack. This wolf's association with the pack was interrupted, however, because of the foot injury sustained during capture. When 1059 was caught, tracks of two other wolves were seen in the immediate vicinity, and one of the animals was seen within a quarter mile of the trapped wolf. Three days after 1059's release, and perhaps sooner, she was back with her pack, with which she remained at least through March.

The detailed histories of the associations of the radiotagged wolves will be discussed in a later section.

Radiotagged wolves were tracked every day that weather permitted during December, January, and February; every week during March, April, and May; and once a month during June, July, and August (fig. 16). Information was obtained for a total of 570 "wolf-days" — a wolf-day being a day in which one radiotagged wolf was located; a pack of five being located for 1 day would constitute 5 wolf-days.

The last day that animals 1051 and 1057 were heard from was April 24, 1969. Both had traveled long distances during the previous week and may have moved out of range. Signals from wolf 1055 were last heard on May 30; this animal had also been ranging widely. Circles with radii of at least 50 miles around the last known locations of each wolf were searched unsuccessfully for the signals. During all subsequent tracking flights for the remaining wolves, the missing animals were also sought, but to no avail. Before the last dates that signals from these animals were heard, attempts to locate marked animals from the air had failed in only three instances.

Daytime Activity Patterns

When radiotagged wolves were located, notes were kept on the type of activity they were engaged in; the results are summarized in figure 17. In a total of 171 observations made between 9:00 a.m. and 6:00 p.m., the wolves were resting 62 percent of the time, traveling 28 percent and feeding 10 percent. They tended to travel more

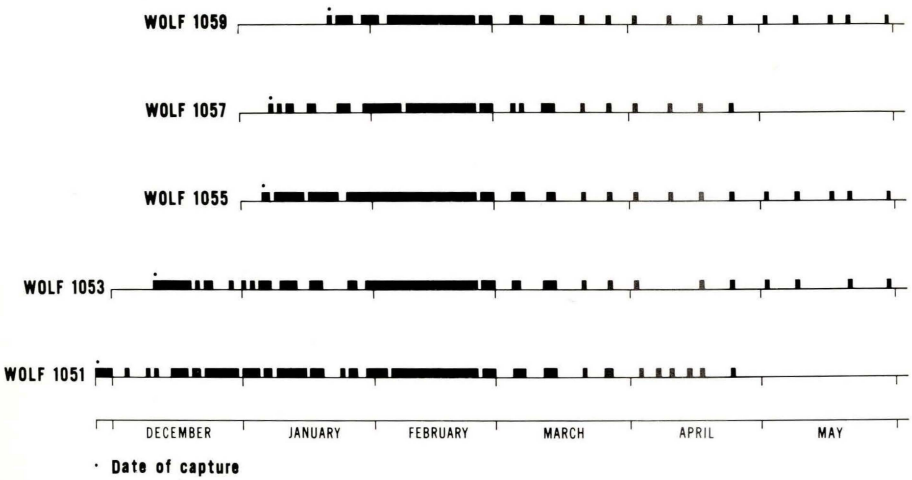

Figure 16.—Distribution of the days on which data were obtained for each of the radiotagged wolves. Because tracking success was 99 percent, this also represents the distribution of effort. During June, July, and August, wolves 1053 and 1059 were located 1 day each month.

before 11:00 a.m. and after 3:00 p.m., although resting still composed at least 45 percent of the activity during every hour (fig. 18).

These results generally agree with the statement by Mech (1966a) that wolves on nearby Isle Royale tend to rest about 11:00 a.m. and begin traveling again about 4:00 p.m. However, it does appear that the Minnesota wolves spend much more of the day resting than do the Isle Royale animals. The difference may be caused by the difference in pack sizes studied. The Isle Royale pack of 15 to 16 may have had to travel more to find enough food to feed all its members than did the lone wolves and pack of five in the present study.

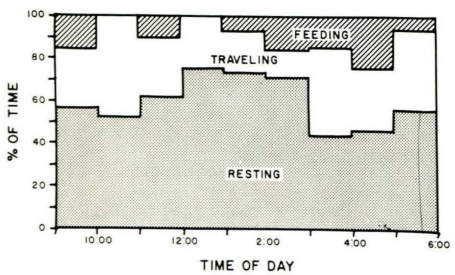

Figure 17.—Percentage of time spent by radiotagged wolves in various types of activity throughout the day, from December through April.

Figure 18.—Generally the wolves rested during most of the day. (Photo courtesy of L. D. Mech.)

Movements and Range

Wolf movement is greatly hindered by deep, soft snow, so during winter travel, wolves frequently use areas where they sink into the snow the least. In our study area, frozen waterways are used extensively where possible, just as reported by Stenlund (1955). Where few lakes or rivers exist, wolves follow railroad beds and logging roads, often soon after a plow or other vehicle has driven on them. In cutting cross country through deep snow, wolves travel single file and tend to stick to windblown ridges and to trails of deer and moose. Wolves that have ranges small enough to cover in a few days form a network of their own trails, which they can maintain merely by traveling regularly over them. Packs on Isle Royale depended a great deal on such a system of trails (Mech 1966a), and so did Pack No. 1059 in our study area.

Wolf packs can travel up to 45 miles in a day but it is usually larger packs that do so (Stenlund 1955, Burkholder 1959, Mech 1966a, Pimlott *et al.* 1969). In our study area we sometimes saw evidence of long moves by large packs along strings of lakes and waterways. However, most of our movement data pertain to lone wolves and a pack of five. The daily travel of these animals was usually much less than that reported for large packs.

Our radiotracking data provide an index to the extent of travel for each wolf rather than the actual amount of travel, for it is based on straight line distances between consecutive points at which an animal was found. This measure will be referred to as the "net daily distance."

Much variation was found in the net daily distances of wolves, with the longest ranging from 4.5 miles for 1057 to 12.8 for 1055 (table 3). The mean net daily distance for each animal, excluding days with no net movement, varied from 1.5 to 3.6 miles. The movements of these wolves may have been affected by the snow depth and penetrability, for mean and maximum net daily distances suddenly increased for all animals between February 23 and 28, when snow penetrability had decreased to a point where walking wolves would be expected to sink in only about 6 inches (table 4). Other possible explanations for the wolves' sudden increase in movements will be discussed below.

The straight line distances traveled between consecutive weekly locations (called the "net weekly distances") showed a similar variation (table 3). The maximum net weekly distance for each wolf varied from 4.6 miles for 1059 to 49.0 for 1055, with means ranging from 2.9 to 15.6 miles for the same wolves. No doubt 1059's net weekly distances were relatively short because her total range and that of her pack were much smaller than those of the other wolves.

It is difficult to obtain comparable measures of the extent of the ranges covered by each of the radiotagged wolves because their patterns of travel varied so much. Thus the figures given in table 5 should be regarded only as gross indicators of the minimum range of each animal. The area figures are especially deceiving in the case of 1055, for she had a horseshoe-shaped range, much of which apparently was not used.

Nevertheless, one major piece of information is obvious from the figures: 1059's pack of five

Table 3.—Straight line distances (miles) between consecutive locations of radiotagged wolves

Wolf number	Net daily distances								Net weekly distances		
	Days data obtained	Days no net movement		Days movement		Mean net distance per day	Mean net distance per day excluding days of no movement	Range	Weeks data	Mean net distance per week	Range
	Number	Number	Percent	Number	Percent	Miles	Miles	Miles	Number	Miles	Miles
1051	54	13	24	41	76	2.0	2.6	0.0-12.0	22	12.7	1.0-46.0
1053	37	20	54	17	46	1.0	2.1	0.0- 5.0	23	6.3	0.0-23.6
1055	46	7	15	39	85	2.9	3.6	0.0-12.8	21	15.6	1.7-49.0
1057	29	11	38	18	62	1.0	1.5	0.0- 4.5	15	4.6	0.0-31.0
1059	26	1	4	25	96	2.5	2.6	0.0- 5.6	18	2.9	0.0- 4.6

Table 4.—Straight line distances (miles) traveled between consecutive days ("net daily distance") by radiotagged wolves in northeastern Minnesota during February 1969

Wolf number	Mean net daily distance		Greatest net daily distance	
	Feb. 1-23	Feb. 23-28	Feb. 1-23	Feb. 23-28
1051	1.1	3.5	2.3	4.8
1053	0.7	2.5	3.0	5.0
1055	2.7	6.2	8.0	12.8
1057	1.0	1.5	4.0	4.5
1059	2.2	3.1	4.0	5.6

Table 5.—Extent of ranges used by radiotagged wolves

Wolf number	Greatest length	Greatest width	Total area[1]	Area[1] of intense use (before late Feb.)
	Miles	Miles	Sq. miles	Sq. miles
1051[2]	28.5	13.6	318	13 (Location A[3]) 45 (Location B) 16 (Location C)
1053	31.1	22.0	392	31
1055	55.4	24.9	997	40
1057	32.3	3.8	77	14
1059[4]	8.4	8.0	43	39

1/ Minimum area method (Mohr 1947).
2/ Before dispersal.
3/ See text and figure 19.
4/ Pack of five.

wolves had a much smaller range than any of the other uninjured animals – approximately 43 square miles when figured by the minimum-area method (Mohr 1947). The next smallest range was that of 1051 (excluding the area of his later dispersal – see below), which was some seven times the size of the pack's range.

There is little published information on the movements and ranges of lone wolves with which to compare our data. Mech (1970) summarized information regarding ranges of packs. Reported ranges varied from 36 square miles for a pack of two wolves in Minnesota (Stenlund 1955) to 5,000 square miles for a pack of 10 in Alaska (Burkholder 1959). Considering only data based on intensive study in the same general region (Minnesota, Isle Royale, and Ontario) as our study area, the largest range reported was 210 square miles for a pack of 15 to 21 wolves on Isle Royale (Mech 1966, Jordan *et al.* 1967). On a per-wolf basis, the ranges in this region varied from 6 to 28 square miles per wolf. Our pack of five with its range of 43 square miles would have about 9 square miles per wolf.

A more accurate assessment of the ranges of the radiotagged wolves requires an individual discussion for each.

No. 1051.—The range of 1051 was composed basically of three distinct areas (fig. 19). Within 10 days after being released, the wolf left the general area of his capture (Area A near Isabella Lake) and traveled to Area B along Highway 1, some 17 miles to the southwest. From December 9 to January 4 wolf 1051 remained in Area B, which covers about 45 square miles. Between January 4 and 6 he returned to Area A and stayed in 13 square miles until February 3. Between February 3 and 5 he shifted to Area C east of Snowbank Lake, 11 miles northwest of Area A. He remained in that 16-square-mile area until February 25, then suddenly left and headed 8 miles to the northeast.

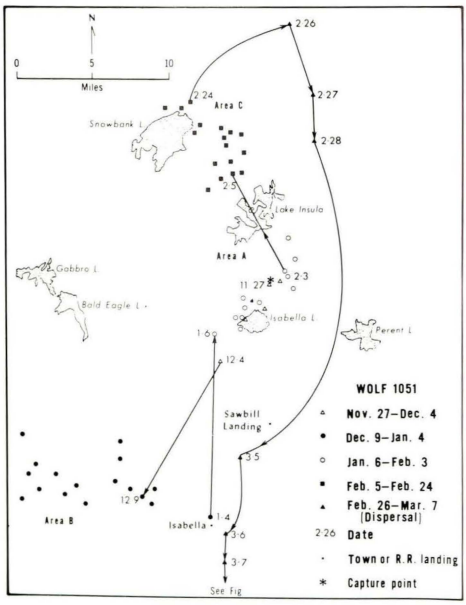

Figure 19.—Locations and range of wolf 1051. Lines are NOT travel routes; rather they merely indicate sequence of locations. Only selected lakes are shown.

From February 26 until April 24 the movements of 1051 were strongly indicative of dispersal (fig. 20). His average weekly straight line move during that period was 25 miles (compared with 6 miles per week before this period), and until March 14 he maintained an almost straight south-southwest heading to a location west of the town of Castle Danger. After that the animal traveled a series of northwest-southwest alternations that on April 3 took him east of Big Sandy Lake to a point 129 miles southwest of where he had begun the dispersal. There he remained for about 2 weeks, but between April 17 and 24 he traveled 26 miles northwest. We last saw him at 3:30 p.m. on April 24 heading northwest through a swamp 15 miles southeast of Grand Rapids, approximately 122 miles from where he had started. The total of straight line distances between 16 consecutive pairs of locations taken at intervals of from 1 to 8 days was 226 miles, which is the minimum distance the wolf traveled during his dispersal.

We observed 1051 for distances of up to 5 miles during these travels; he maintained a steady trot that seemed faster than usual, and he appeared intent on heading in a straight line. He did chase deer during his travels, and twice was seen feeding on carcasses. In the area where he remained for about 2 weeks, he was twice seen closely associated with another wolf. This relationship will be discussed later.

An extensive search was made for 1051's signals on May 2 in an area of at least 50 miles radius from his last known location, but it was unsuccessful. On each subsequent tracking flight, the wolf's frequency was also monitored with no success. Possible explanations for the loss of the signal from this wolf include the following: (1) premature expiration of the transmitter, (2) capture of the wolf and breakage of the transmitter, (3) loss of the exposed antenna and consequent reduction of range, and (4) travel of the wolf out of range of the tracking aircraft.

During 1051's travels a number of interesting events took place:

Nov. 27, 1968 – Captured and radiotagged
Dec. 4, 1968 – Crossed road in front of tracking truck
Dec. 8, 1968 – Moved to Area B
Dec. 9, 1968 – Surprised on the ground at distance of 35 feet
Dec. 18, 1968 – Chased by loggers with axes

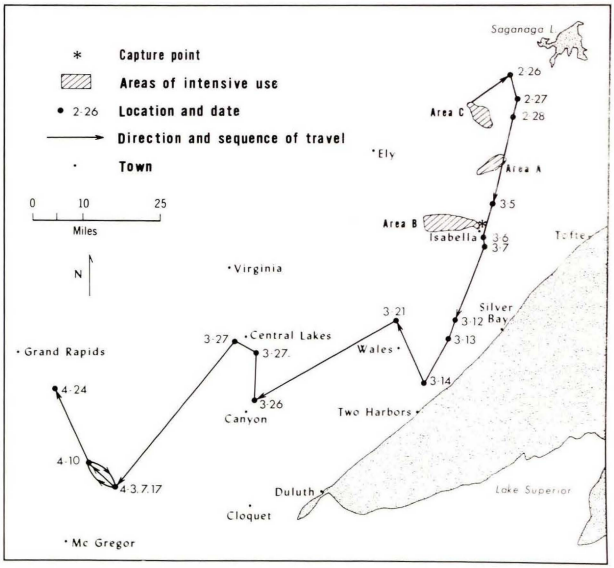

Figure 20. – Dispersal of wolf 1051. Lines merely indicate sequence of locations. Only selected lakes are shown.

Dec. 25, 1968 – Almost shot by trapper who saw collar and withheld fire
Jan. 5, 1969 – Returned to Area A
Jan. 13, 1969 – "Bumped" twice on logging road by loggers in auto but no apparent injury
Feb. 4, 1969 – Moved to Area C
Feb. 26, 1969 – Began long-range southwest movement considered to be dispersal
Mar. 14, 1969 – Seen feeding on old carcass within 200 yards of houses, dogs, and a man walking
Mar. 27, 1969–Chased two deer across 4-lane State highway 53
Apr. 3, 1969 – Found with another wolf at point farthest south in his range
Apr. 24, 1969 – Last contact with this animal; was seen traveling NW

Wolf 1053.–This wolf was basically a scavenger who subsisted for long periods on the remains of old carcasses. She was known to have visited the remains of at least four deer and three moose, and she stayed near one moose carcass from February 8 to 20, at least during the day. Between her date of capture, December 10, and February 28, 1053 traveled about in an area of 31 square miles in the Arrow Lake-Maniwaki Lake region (fig. 21).

Between February 28 and March 6 she suddenly moved 13 miles to the east-southeast near the Sawbill Trail, and during the next week she traveled a straight line distance of 24 miles southwest to a point southeast of the town of Isabella. Her subsequent travels eventually took her over a much larger area. Before February 28, 1053's average weekly straight line distance was 2 miles, but after that date it increased to 11 miles.

Wolf 1055.–The range of this animal from January 5, when she was captured, to February 23 covered about 40 square miles near Stony Lake, Slate Lake, and the Jack Pine Lookout Tower (fig. 22), and her mean weekly distance was 4 miles. Between February 23 and 24, however, she traveled 13 miles northeastward, the beginning of a series of long moves. By March 5, 1055 had reached Crescent Lake, a point 39 miles east-northeast of her previous area of intensive use. She then gradually headed back toward the west and south during the next 10 days and within the next month repeated this pattern. When her signal was heard last on May 30, 1055 was near Martin Landing in the center of her range. Her mean net weekly distance after February 23 had increased to 22 miles.

Wolf 1057.–The movements of 1057 cannot

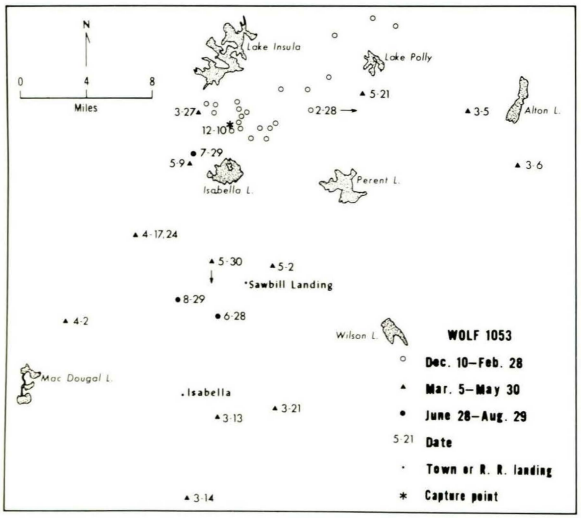

Figure 21. — Locations and range of wolf 1053. Only selected lakes are shown.

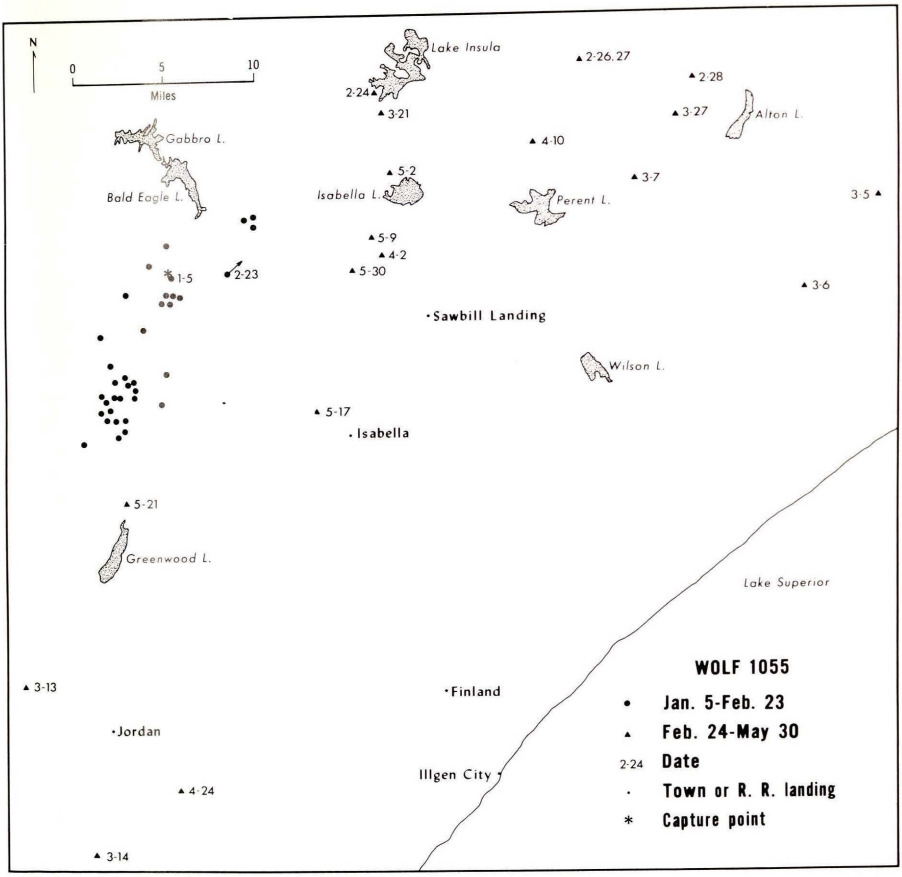

Figure 22.—Locations and range of wolf 1055. Only selected lakes are shown.

be considered normal because freezing of a front foot prevented her accompanying the pack of which she was a member. Nevertheless, even data from an abnormal animal can provide some information. On January 13, 5 days after capture and release on Red Rock Lake, 1057 was located 4 miles from the capture point with a pack of 10 other wolves. She was limping and fell behind when they moved. Five days later she was again seen with the pack 12 miles away between Knife Lake and Kekekabic Lake. She then remained in about 14 square miles of that general area through April 17 (fig. 23).

Suddenly on April 24, 1057 was found in Ontario some 31 miles northeast of her location of the previous week. That was the last time we heard her signal even though on May 2 we scanned an area with a radius of 35 miles from her last known location and listened for her signal during every subsequent flight.

Wolf 1059.—This animal was a member of a pack of three to five wolves (see next section). The movements of the group varied little and were concentrated in the August Lake, Omaday

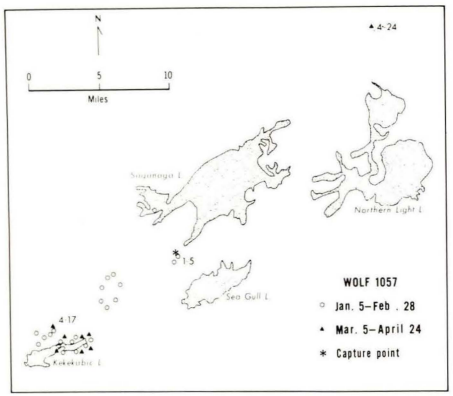

Figure 23.—Locations and range of wolf 1057. Only selected lakes are shown.

Lake, and Keeley Creek area in about 43 square miles (fig. 24). Contrary to animals 1051, 1053, and 1055, this pack did not suddenly begin a series of longer weekly movements in late February. Both before and after February 28, the average weekly straight line movement of the pack was just less than 3 miles.

Probably these animals did begin traveling more in late February, for their net daily distances did increase at that time along with those of the other wolves (table 4). However, the increased travel took place within the restricted area of the pack's usual range rather than in new areas as occurred with the other wolves.

Because 1059 was later found to have bred and carried five fetuses, her movements during whelping season (late April and early May) are of interest. Her locations on both April 24 and May 2 were within 250 yards of each other, which might indicate that she was denning. On May 9, however, she was 2.5 miles east of these locations, on the 17th and 21st was 2 miles west of them, and on the 30th was 3 miles north of them.

In early January 1970, Wolf 1059 was killed by a trapper in the southeast corner of her pack's 1969 range.

Summer locations.—Signals from only 1053 and 1059 were heard during summer, and then tracking attempts were made only on June 28, July 29, and August 29. Locations for 1053 on those occasions were near Kelly Landing and Isabella Lake, within her previous range. Wolf 1059 was found each time within 2 miles outside of the southwest corner of the pack's winter and spring range.

Wolf Associations, Social Behavior, and Reproduction

In our study area, population units of wolves exist as both single animals (lone wolves) and packs. In a total of 77 observations, lone wolves constituted 32 percent of the sightings (fig. 25), with packs of from 2 to 13 members making up the remainder (Table 1). On the basis of the

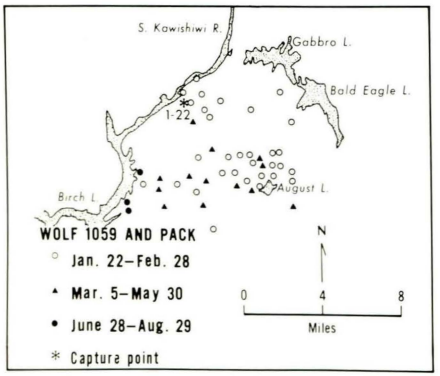

Figure 24.—Location and range of wolf 1059 and pack. Only selected lakes are shown.

Figure 25.—Only 8 percent of the wolves observed were lone wolves. (Photo courtesy of L. D. Frenzel.)

number of wolves seen, rather than the number of observations, lone wolves accounted for only 25 (8 percent) out of 323.

These figures compare favorably with reports in the literature as summarized by Mech (1970). In five areas studied, lone wolves made up from 24 to 60 percent of the observations of population units, and from 8 to 28 percent of the wolves seen. In our study area during 1948 to 1953, lone wolves constituted 43 percent of the observations and 15 percent of the wolves (Stenlund 1955).

The average size of the population units observed during our study (total number of wolves seen divided by the number of observations) was 4.2, which is significantly larger (95 percent level) than the average seen in this area (2.8) from 1948 to 1953. This is also larger than that reported from any other area of comparable size (table 6).

Table 6.—Mean sizes of wolf population units reported from various areas

Area	Observations	Wolves	Mean size of population unit	Largest pack size	Authority calculated from
	Number	Number			
Alaska	310	1,041	3.4	12	Kelly 1954
Alaska	1,268	4,823	3.8	21	R. A. Rausch[1/]
Lapland	118	311	2.5	12	Pulliainen 1965
E. Finland	460	984	2.1	12	Pulliainen 1965
Minnesota	112	318	2.8	12	Stenlund 1955
Minnesota	77	323	4.2	13	Present study

1/ R. A. Rausch. Personal correspondence to L. D. Mech, 1967.

The largest pack seen in our study area included 13 members, and there apparently were at least two such packs. Although larger packs than this have been reported, any group containing more than 8 to 10 members is unusually large (Mech 1970).

Wolf sociology is a complex subject and is still not well understood, so the following detailed observations of the associations between our radiotagged wolves and others are given. Associations are defined as relationships in which two or more wolves relate in a close, positive manner.

As mentioned earlier, 1051 may or may not have been associated with other wolves when he was captured. However, although this animal was observed 55 times throughout winter and spring, only twice was he seen associating with another wolf. Probably the same individual was involved each time, because the location was about the same (the vicinity of the juncture of Aitkin, Carlton, and St. Louis Counties).

The first occasion was on April 3. Wolf 1051 in the previous week had moved 46 miles straight line distance from the northeast. He was then observed lying peacefully within 15 feet of another wolf near a freshly killed deer. The very proximity of the two animals implied a positive relationship. On April 7, 10 and 14, 1051 was seen 1 mile, 10 miles, and 8 miles from the kill and was alone each time.

However, on April 17, 1051 was back in the general vicinity of the kill, and he and another wolf were resting on an open hillside about 100 feet from each other. As we descended for a closer look, the smaller animal arose and headed to the larger, presumably 1051 because he had not been disturbed by the aircraft. The larger wolf did not arise for several seconds, but eventually followed the other into the woods. No tail raising or other expressive posturing was seen in either wolf. One week later 1051 was 26 miles northwest of the kill traveling alone.

Wolf 1053 was never seen less than 80 yards from another wolf, and there was no evidence that she ever associated with a conspecific. Even when she was seen 80 yards from the other wolf, both were resting, and when the strange wolf left, 1053 made no attempt to accompany or follow it.

No. 1055 apparently had been traveling with another wolf when caught on January 5, and tracks showed that the individual had remained near her until we arrived to handle her. Tracks found on January 7 and 10 suggested that 1055 was with another animal, but that animal was not seen during any of the six times 1055 was observed through February 1. However, from February 5 to 19, 1055 was with another wolf on eight of the 12 times she was seen. The two animals were observed resting, traveling, hunting, and feeding together. On February 20, and thereafter, 1055 was alone all 14 times she was seen.

It is possible that 1055's associate was killed between February 19 and 20.. About March 6, a 63-pound male wolf pup was found dead (by Mr. Charles Wick, USDA Forest Service) within about 50 feet of a highway and less than a mile from where 1055 and her associate were seen on February 19. Because of the snow conditions, it was judged that the wolf had been killed (prob-

ably by an automobile) sometime in February.

Wolf 1057, whose foot froze during capture, was a member of a pack of 10 to 13 wolves, and was seen with the pack on January 13 and 18. After that she was usually found alone, although on at least five occasions she was with one or more wolves:

Period	No. of observations	Associations
Jan. 13	1	10 other wolves
Jan. 14-17	1	None
Jan. 18	1	10 or 11 other wolves
Jan. 19-29	2	None
Jan. 30	1	1 other wolf
Jan. 31 to Feb. 2	2	None
Feb. 3-4	2	2 other wolves
Feb. 5	1	1 other wolf
Feb. 6-13	6	None
Feb. 14	1	3 other wolves
Feb. 15-22	5	None
Feb. 23	1	10 to 13 other wolves
Feb. 24 to Apr. 24	6	None

February 23 she was with the pack at a kill in her usual area, and although the pack left that night, 1057 remained near the kill the next day. Presumably this animal would have traveled with pack if she could have.

No. 1059 was part of a pack that included three to five members (fig. 26). From January 25, the first time she was observed after release, through April 2, the animal was seen 19 times with two other wolves, eight times with at least three others, and eight times with four others. She was never seen alone until April 17; both times after this when she was seen, May 9 and 21, 1059 was also alone.

Some insight into the fluctuating size of this pack was obtained on February 27 when the five animals were followed for 2 hours. During that time two members (one of which was larger than the other) often lagged behind the other three by as much as a mile. These two romped and played considerably, with one carrying a stick or a bone part of the time. Eventually they caught up again to the other three. The behavior of the two lagging wolves would be consistent with the hypothesis that they were either pups or a courting pair of adults. In either case, they seemed to be an actual part of the pack even though they temporarily traveled separately.

Figure 26.—One of the radiotagged wolves was a member of this pack of five. (Photo courtesy of L. D. Mech.)

The fact that 1059 was observed traveling alone three times from April 17 to May 21 may be further evidence that the pack had a den in the area at that time. The presence of a den allows individual pack members to venture off singly and return each day to a known social center, as Murie (1944) observed, so they do not need to travel with each other to maintain social bonds. Wolves in our area breed during the latter half of February (see below), and the young should be born in the latter half of April. Since dens are prepared a few weeks in advance (Young 1944), pack members might be expected to begin traveling singly in mid-April.

Some information on social relations within our radiotagged pack of five was also obtained.

One of the members could often be distinguished from the others by its reddish cast and this individual appeared to be the pack leader or alpha male (Schenkel 1947). In urinating, this animal lifted his leg, a position seen almost exclusively in males. Except for only two temporary occasions, this animal always headed the pack, which usually traveled single file. The second wolf in line generally was noticeably small, possible a female, and the third wolf was twice identified as 1059 on the basis of sightings of her collar.

The leader often gained a lead on the other wolves, especially during a chase (see below), much as reported for a lead wolf on Isle Royale (Mech 1966a). Upon returning to the lagging members of the pack, this animal usually held his tail vertically, an expression of social dominance (Schenkel 1947). On two occasions he led chases against strange wolves and demonstrated the highest motivation (see below).

The leader was also the most active in his reactions when scent posts were encountered. Because the function of scent-marking behavior is still unknown, it is important that detailed descriptions of the natural behavior of free-ranging wolves around scent posts be made available (fig. 27). Thus the following excerpt from field notes by Mech dated February 27, 1969, is presented:

> "When they [the three wolves] came to a small frozen pond, where the wolf trail [which they had been following] branched and there were some packed down areas, they became quite excited [fig. 28]. This was especially true of the reddish wolf. He nosed several spots, and scratched around them. Usually his tail was vertical. He defecated at one spot, and right afterwards another wolf did. After about 2 minutes that pack went on.
>
> "About 15 minutes later the 2 'satellite' wolves arrived at this spot, hesitated, nosed around but continued on after less than a minute.
>
> "The three wolves meanwhile came to a junction of 2 logging roads. There they nosed around, scratched, and acted much as described above. Again the reddish wolf was most active and had its tail up.
>
> "When the last 2 wolves came to this spot, they nosed around, ran back and forth, and 1 defecated. They then headed on a different branch of the trail than the first 3 had gone on just 10 minutes before.
>
> "The first 3 wolves meanwhile were running along a logging road but eventually they circled and one other than the reddish one headed across a swamp toward the last 2. Then the reddish one and the other followed this one, and they met the last 2 on a ridge. There was the usual tail wagging, then all headed off together in a new direction. They passed the first scent post again and there was some nosing by the reddish wolf but little hesitation.
>
> "When they traveled, one wolf lagged behind by 150 yards. The wolf just ahead of it had its tail vertical part of the time, as did the reddish leader.

Figure 27.—Feces, urine, and scratching in a conspicuous spot indicate a wolf "scent post." (Photo courtesy of L. D. Mech.)

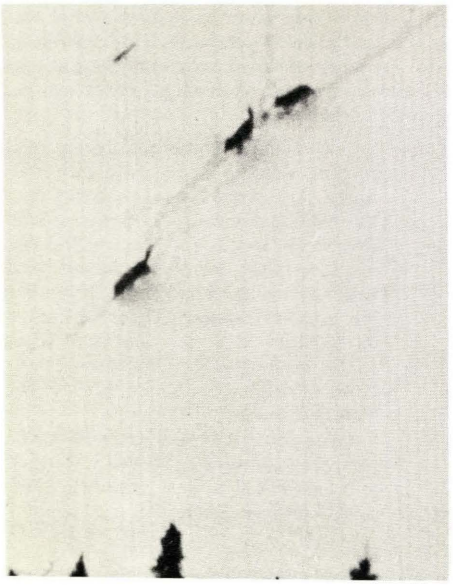

Figure 28.—A pack of wolves investigating a scent post. The raised tails indicate their excitement. (Photo courtesy of L. D. Mech.)

> "Soon the pack came upon another area packed with wolf tracks on a pond. There they followed every little trail, nose to the ground, wagged tails, grouped together often, chased each other, rolled over, etc. for 6 minutes. The reddish animal had tail up most of the time.
>
> "The wolves continued on, and we left them about 1 mile S.W. of the S.W. arm of Bald Eagle Lake [at 6:05 p.m.]."

Unfortunately it was not known whether the trails that the wolves were following were their own or those made by other wolves.

Significant aspects of the above observation are (1) the spirited initiative of the leader, (2) the amount of time spent in scratching, urinating, and defecating, (3) the decision of the last two wolves to take a different route from that of the first three even though their goal seemed to be to catch up to the first three, and (4) the fact that the scent posts were located at trail junctions. In the last regard, we often noted from the ground that wolves urinated at the junction of newly formed human trails heading perpendicularly from roads they were following.

Copulation in wolves was only observed once during our study, on February 19, 1969. Two members of a group of four were seen coupled for 2 minutes on Kekekabic Lake. On Isle Royale, which is at the same latitude, copulations were witnessed on February 21, 24 and 27 (Mech 1966a).

On April 17, a den west of Big Moose Lake known to have been used at least intermittently for 13 years was seen from the air to have fresh activity of some kind in the snow in front of it, and on April 24 we saw a wolf at the mound. A few days later, two local human residents unaware of our interests approached this den and looked in. An adult wolf, presumably the bitch, leaped over their heads and fled the area. The men then dug up the den and removed six pups whose eyes had not yet opened.

Intraspecific Intolerance and Indifference

Instances of chasing or attack by a pack of wolves on conspecifics not a part of their group have been described by Murie (1944) and Mech (1966a). Observations of such behavior are important in trying to determine conclusively whether or not wolves are territorial. Pimlott *et al.* (1969, p. 75) wrote "It still is not clear, however, whether or not their use of range should be defined as territorial." Mech (1970) summarized the available evidence for territoriality in wolves and postulated that it may be spatiotemporal such that packs might avoid each other at any particular point in time but over a long period might cover the same area at different times. A number of our observations are pertinent to this question, for we have evidence of both tolerance and intolerance between population units of wolves.

Two direct cases of intolerance were observed, both involving the radiotagged pack and other wolves within the usual range of the pack. Following is a direct quote from the field notes of Mech:

> "Feb. 7, 1969—about 11:30 a.m.—aerial and visual—1059 and 2 other wolves traveling overland about halfway between Heart L. and August L. (R10W-T61 N.

Sect. 17 center). They were traveling quickly and intently along a fresh wolf trail, with a lighter reddish individual in the lead. The other 2 animals were darker colored, and one of them was smaller than the other. One of them must have been 1059.

"We soon found that about half a mile ahead of the pack was a dark wolf hurrying away from the three. This animal often looked back and ran whenever it encountered good running conditions. It soon became obvious that the pack of 3 was chasing this individual. Because it [the lone wolf] often broke its own trail, the pack gradually gained on this animal. The single wolf flushed a deer which ran when the wolf was about 75 feet away and floundered in the snow, but the wolf continued hurrying on by.

"Although the deer ran only about 50 yards and stopped, the pack of 3 also hurried on by. The single wolf flushed another deer, ignored it, and continued by, as did the pack of 3. The chase continued for 2 miles as we watched, into the N.E. corner of Sect. 18 and then into the N. Central part of Sect. 8, and the pack got to within 150 yards of the single wolf.

"However, at this point, the 2 darker members of the pack had fallen about 100 yards behind the lead one. The lead animal stopped and waited for them, as it had done a few times before. It then turned around and headed back to these animals. When they met, the reddish animal's tail was held vertically and there was much tail wagging by all for about 1 minute. Then all animals lay down for a minute and then went up on a knoll. There was much activity and 'playing' on the knoll. (12:10 p.m.)

"The single wolf continued running and looking back for at least another mile. We left at 12:21 p.m.

"At 4:07 p.m. we saw a single wolf running across a small lake and looking behind it about 8 miles N.W. of these animals. The creature behaved the same as the one being chased today, and we wondered whether it could be the same animal."

On February 18, 1969, Ream made a similar observation, as follows (quoted from his field notes):

> "Got visual sighting on 1059 with 3 other wolves at 11:55 about a mile west of Omaday Lake and they were running along fairly fast on a trail. When we circled a second time we saw 2 wolves curled up sleeping on a knoll ahead (south) of the running pack. We then realized the running wolves were on the trail of the sleeping wolves and when the pack of 4 with "red" in the lead was about 50 yards from the knoll the 2 sleeping wolves jumped up and charged away in the opposite direction full tilt, and split and went in 2 directions. When the pack reached the knoll they started off on the trail of the wolf that headed N. E. and then changed and went after the one that headed S. W. The reddish wolf was in the lead and really picked up the pace. Although the reddish wolf seemed to gain on the chased one 3 or 4 times, the pack as a whole couldn't catch up, even though the single was breaking trail. The reddish wolf, after gaining, always stopped and waited for the others or went back to find them. They chased this wolf for 2½ to 3 miles, all the way down to Highway 1 at a point 3.0 miles from the lab [Kawishiwi Field Station, U.S. Forest Service]. There was a dense patch, 10-15 acres, of woods just before Highway 1 and we lost sight of the chased wolf for a while and also the 4 when they entered it, but shortly we found that the chased one had somehow doubled back and was heading N.E. again. The pack was apparently confused for at one point 3 of them were wandering back and forth on Highway 1, apparently looking for the trail of the chased wolf. Two of these paralleled the Highway for a couple hundred yards and then stopped on top of a hill, apparently resting. During this chase both the single wolf and the pack chased up deer from their route of travel and didn't seem to

pay much attention to them, even though some were really floundering in the deep snow. We finally stopped watching all of this at 1:30 p.m. and proceeded on our rounds."

On February 21 we also saw a single wolf running and looking behind several times on Ojibway Lake. Even when it saw a fisherman on the lake within ⅛ mile, it continued across to the opposite shore seeming most intent on avoiding whatever was on its trail. Presumably it had also been chased by a pack.

The cases of tolerance or indifference that we witnessed between wolves involved our lone animals. On January 27, 1051 was at a kill he had made the day before, and another wolf was sitting within 100 feet looking toward the carcass. Eventually the unidentified wolf left without approaching any closer. A lone wolf was also seen near 1053 in the general vicinity of a moose carcass, which probably both were feeding on at different times. Three such observations were made, on February 10, 15, and 18; and on February 21 another wolf was also seen near 1053 some 2.5 miles away from the moose carcass. In all cases, the two animals were 80 to 200 yards apart in open country and must have been aware of each other's presence.

Hunting, Killing, and Feeding Behavior

The primary prey of most wolves in our study area is the white-tailed deer (fig. 29), but some moose (fig. 30) are also killed. We have examined the remains of six moose that were eaten by wolves, two of which were killed by them (fig. 31). One was found on February 25, 1967, on Gillis Lake and the other on March 7, 1969, on Twinkle Lake. These locations are within 3 miles of each other, suggesting that a wolf pack in that area may be more accustomed to preying on moose than other packs. The other four moose carcasses were found in other parts of the study area, but circumstances were such that the causes of death of those animals could not be determined. A discussion of the details of wolf-moose relations in our study area must await the collection of additional data.

The remains of 93 wolf-killed deer, and 49 probable wolf-kills, were examined for age, sex, and condition and were compared with a sample

Figure 29.—The main prey of wolves in northern Minnesota is the white-tailed deer. (Photo courtesy of L. D. Mech.)

Figure 30.—Moose are also killed by wolves. (Photo courtesy of Allan Taylor.)

Figure 31.—Only a few wolf-killed moose were located during the study. (Photo courtesy of Laurence Pringle.)

of 433 hunter-killed deer from the same general area. The wolf-killed deer were generally much older than the hunter-kills and had a significantly higher percentage of jaw and limb abnormalities (see Mech and Frenzel, page 35).

Until recently the only observations of wolves hunting deer were those reported by Stenlund (1955) for northern Minnesota. He described two reports of actual observations and two reports of interpretations of tracks in the snow, all successful hunts. Since that time several descriptions of successful and unsuccessful hunts have also been published (Mech 1966b, Rutter and Pimlott 1968, Pimlott *et al.* 1969, Mech 1970). Nevertheless, many more observations must be made before generalizations can be formed.

During the present study we were able to witness a number of hunts from the air and piece together others based on tracks. The following descriptions are quoted from the field notes of Mech:

> "26 January 1967. About ¾ mile N.E. of Alice Lake.
>
> "Jack Burgess [pilot] and I were following a pack of 8 wolves, when at 4:15 they veered from their former line of travel, about 30°. They were then about 200 yards from 2 deer. They began wagging their tails when about 175 yards from the deer. One deer, on the edge of a steep bank, was lying, but one was standing about 75 yards N. of it in open hardwoods. The wolves continued toward the latter deer.
>
> "This deer remained standing in the same place until the wolves approached to within about 100 feet of it. The lead wolf stopped, when that distance from the deer, and the others caught up but also stopped when within about 25 feet behind the lead wolf. By this time the deer, whose body was facing away from the wolves, had its head turned back over its shoulder toward the wolves. The wolves and the deer remained absolutely still while staring at each other, 100 feet apart, for 1-2 minutes, while we made several circles.
>
> "Suddenly the deer bolted, and instantly the wolves pursued. I am fairly certain that it was the deer that bolted first, but could be mistaken. The action was almost simultaneous. The deer headed toward the other deer near the top of the high bank. This animal had been lying but had arisen when the wolves were about 150 yards away.
>
> "The lead wolf followed in the deer's trail, but the others cut toward the bank. This flushed the second deer (near the edge of the bank), which ran down the bank. Meanwhile when the first deer reached the edge of the bank, it headed due W. along the top of it. Only the lead wolf pursued this animal. The other deer had headed down the bank to the S.E., and at least a few of the wolves followed it.
>
> "We could not watch both deer, so we continued following the first. The deer had no trouble in snowdrifts, but the wolf was hindered by them. The wolf followed the deer for about 200 yards along the top of the bank, and then gave up after losing ground. The wolf had run a total distance of about 250-275 yards. He then lay down and rested.
>
> "We noticed at least 3 wolves stopped part way down the bank in the trail of the second deer. However, we did not

see the remaining wolves or the second deer.

"Eventually (after about 5 minutes), these wolves joined the first, and all rested. At 4:25 p.m., one wolf started toward a third deer, which had been lying under a tree while the former chase took place. The deer was about 150 yards from where the wolves rested, and it had stood before the wolf started toward it. We could not see whether the deer or wolf bolted first, but suddenly both animals were bounding away. The wolf chased the deer about 125 yards and gave up after losing ground. The other wolves followed slowly in its trail, and all assembled and rested. The deer continued running for at least ¼-mile."

"27 February 1969. 2 miles N. of August Lake.

"1059's pack of 5 was heading N.E. at 4:10 p.m. when they got to within 100 yards of 2 standing deer. The deer had been standing alertly in a shallow draw, and when at least 2 wolves got to within 100 yards, they fled. The wolves began running after them.

"The deer were in snow up to their bellies and had to hesitate slightly at each bound. But they ran fast. We could only see one wolf very much [of the time]. It was also having a difficult time in the snow, and after a total run of about 250 yards (100 to the deer's original location and 150 after the deer), the wolf lay on the snow and rested about 10 minutes. The deer ran only about 200 yards more and stood alertly for the next 20 minutes at least. The wolves then went on.

"27 March 1969. About 2 miles S. E. of Central Lakes, Minnesota.

"At 3:00 p.m. while we were following wolf 1051 by aircraft in above location, we saw a deer running very quickly on top of the crusted snow and then stand and watch its backtrail. About 1½ minutes later we saw 1051 running along the same route. We did not see when the deer fled again, but saw it running about 100 yards from the wolf and doubling back paralleling its original route. When the wolf got near the approximate doubling-back point, he lay down and rested for about 5 minutes. The deer continued fleeing for about 350 yards, stopped, and for several minutes faced its backtrail. The wolf finally continued on in his original direction, giving up the chase.

"At 4:30 p.m.—1½ miles S. of Central Lakes, Minnesota—Wolf 1051 had come to within 100 yards of [four-lane] Highway 53 and was hesitant to approach it. Several cars were going by in both directions. Thus the wolf headed S. parallel with the highway about 150 yards E. of it.

"Suddenly two deer, which we had noticed S. of the wolf earlier, fled across the highway. The wolf soon got to the point where they crossed, hesitated about a minute and then ran across. No cars came at that time.

"We could not always see the deer or the wolf when W. of the road because there were several patches of evergreens. The wolf did head straight W. after crossing the road. Then about 250 yards W. of this point we saw a deer come out onto an old woods road which lay in a N.W.-S.E. axis. The deer ran N.W. on the road and then we saw the wolf where the deer had come out onto the road. While the deer ran N.W., the wolf cut into the woods to his right, N.E. We could not see it then but presumed it was running N.W. paralleling the road.

"After the deer had run about 50 yards up the road, it also headed N.E. into the evergreens. Within a few seconds it fled right back out and started S. E. down the road. The wolf was about 50 feet behind it and began gaining.

"When the deer got back to where the wolf had headed into the woods from the road before, it also headed N.E. into the woods. The wolf was then about 20 feet away and the deer was headed N. around in a circle with the wolf closing in on the outside. The wolf did not emerge from the evergreens for at least 15 min-

utes, nor did we see the deer, so I presume the wolf killed the deer. [But see entry for April 1.]

"1 April 1969. Dan Frenzel and I searched the area described on March 27 for 1 hour and found no sign of a kill. Old wolf tracks were seen, but only a single wandering track. No concentration such as usually seen at kills. Best conclusion is that 1051 did *not* kill the deer where seen from the air March 27."

We also saw 1055 and her associate actually kill a deer, on February 6, 1969, but we did not realize what was going on and it happened so fast that we only saw a wolf rushing and biting at the front end of the downed animal. The chase had to have lasted only a few seconds.

In addition to the above direct observations, we also were able to piece together from tracks in the snow the chase and successful encounter between a single wolf and a deer in two instances. In the first case, on January 25, 1967 (11:50 a.m.), we arrived at the scene (near Grub Lake, just N. of Snowbank Lake) within an hour of the encounter, and the wolf was still feeding on the deer, which had been a 2½-year-old female. Mech examined the area from the ground and made the following observations:

"The deer had come S.W. down the middle of the lake at a fast walk, turned around, backtracked a few yards and headed to the N.W. shore of the lake. Meanwhile a wolf had come at a trot along the deer's track, but it had cut to the N. W. shore about 50 yards N. E. of where the deer had. When still on the the ice about 15 feet from shore, the wolf began running as evidenced by his long bounds. He continued running inland about 50 feet from shore toward the deer. The deer had walked inland from the shore and may have stood there about 25 feet from shore. Suddenly it had bounded away. The bounding wolf track was in the same trail as the deer's for about 25 yards but then it paralleled the deer's about 5 feet away on the inland side. After about 125 yards from where the deer flushed, the deer was pulled down. It was *not* on its side but rather had sunk into the snow in more-or-less of an upright position.

"Apparently the deer had just about reached the shore when the wolf noticed it, and it detected the wolf. At this time the wolf must have been up the shore about 50 yards where his tracks first showed he began bounding. There was no sign that the wolf had spotted the deer on the lake and had tried to cut it off from shore by running inland along the shore and then waiting for the deer to come inland. Once the wolf had begun bounding, he continued until he pulled the deer down . . . Sign showed that the deer dropped within about 20 feet of where she had begun bleeding."

The second case involved a 5½-year-old buck, No. M-28, which had arthritis of his right hind foot and probably had defective gait (see Mech and Frenzel p. 35). The attack took place on Basswood Lake on February 2, 1967, and excerpts from field notes by Mech follow:

"A single wolf had killed this deer after chasing, following, or tracking the deer about 3.75 miles. The deer's last 350 yards was a fast walk – the tracks were one in front of the other and about 2 feet apart, and there was no leaping or bounding. Same with the wolf – a fast trot.

"Where the tracks came together, the deer apparently had fallen, but there was no blood. From there, the deer dragged its feet or the wolf for about 25 feet and then went down again. The wolf circled the deer, and for the next 150 feet, the 2 animals had fought or scuffled and then the deer had gone down where we found it.

"The 4-mile persistence of this wolf—whether tracking, following, or chasing the deer—is remarkable [compared with most chases] and makes me believe the wolf had good reason to believe it could kill the deer."

Our observations of wounds on fresh kills confirm the following description by Stenlund (1955, p. 31) of the location and manner of attack of wolves on deer: "No evidence of hamstringing of deer was found on freshly killed carcasses, although the possibility does exist. Usually deer are run down from behind, the

wolf or wolves biting at the hind flanks and abdomen, or at the hind flanks and head region simultaneously."

On each kill, all the flesh and much of the skin and bones were eaten, at least during the winters of 1966-67 and 1967-68. This was also true during December 1968 and much of January 1969. However, during February and March 1969 when an unusual accumulation of snow had built up, most of the kills were only partly eaten (see Mech *et al.*, page 51). In previous years deer freshly killed by single wolves were sometimes found with only a few pounds of flesh or viscera missing. However, in each case the carcasses were almost completely cleaned up within a few days, often by packs to which the single wolves may have belonged (Mech 1970).

Usually the first parts of a carcass to be eaten are the hams and part of the viscera from the coelomic cavity. In one case where a wolf was interrupted while feeding it was apparent that the animal had been stripping the omental fat from the carcass. This may be the wolf's favorite part of a deer, for the stomach of one wolf that we examined in January 1967 contained nothing but such fat.

The average consumption and kill rate of deer by wolves has not yet been determined, but we have some information bearing on the subject. Because our data were obtained during a winter of unusually deep snow, and it was obvious that wolves were killing more deer than they could eat at the moment (see Mech et al., page 51), our figures should be considered much higher than average. However, they should be useful in that they probably represent the maximum kill rate not only throughout the year but also throughout a period of many years.

By observing each of our radiotagged wolves whenever possible and noting whether or not it was feeding on a kill, we learned that our wolves generally remained close to their kills for periods of from 1 to 7 days, depending on how recently they had eaten (fig. 32). Thus, when a wolf was found at a new location each day, the assumption could be made that the animal did not currently have a kill.

We assumed that wolves found at fresh kills (fig. 33) had made them unless there was evidence to the contrary as with 1053, the scavenger. When a wolf was found at one location for several consecutive days but could not be observed, we assumed it was feeding on a kill, since whenever wolves were observed remaining in the same location for several days they were seen feeding. Thus a range of possible number of kills per wolf was determined, with the lower limit being the known minimum and the upper limit the possible maximum. When more than one wolf fed on a kill, as with the pack, the figures were calculated on a per-wolf basis.

In this way we obtained data on a total of 468 wolf-days and found a total kill of 35 to 48 deer (table 7). This averages out to a kill rate of one deer per 10 to 14 days per wolf. The figure varied considerably among individuals –

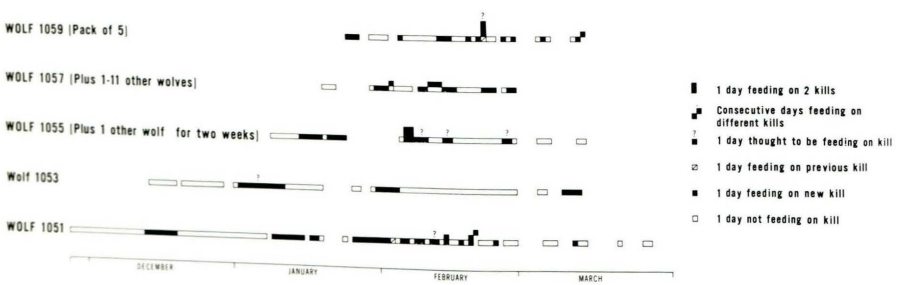
WOLF 1059 (Pack of 5)
WOLF 1057 (Plus 1-11 other wolves)
WOLF 1055 (Plus 1 other wolf for two weeks)
Wolf 1053
WOLF 1051
DECEMBER
JANUARY
FEBRUARY
MARCH
1 day feeding on 2 kills
Consecutive days feeding on different kills
1 day thought to be feeding on kill
1 day feeding on previous kill
1 day feeding on new kill
1 day not feeding on kill

Figure 32.–Periods spent by radiotagged wolves and their associates feeding on kills judged to be their own. This does not include periods when they were known to be feeding on carrion.

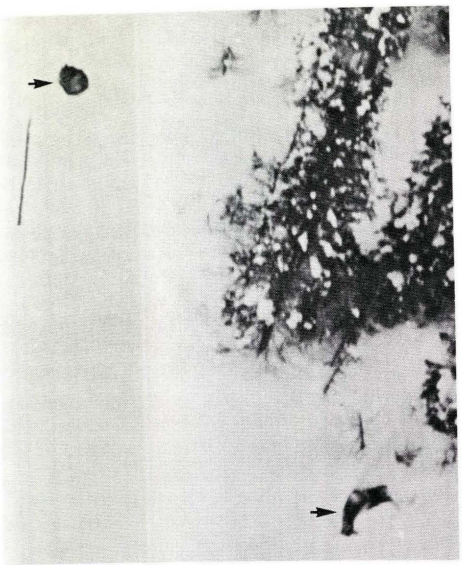

Figure 33.—Radiotagged wolf (upper left) found at kill (lower right). (Photo courtesy of L. D. Frenzel.)

1051 had the highest rate of one kill per 6.3 to 7.2 days, and each wolf in 1059's pack had the lowest rate (except for 1053, the scavenger) of one deer per 14.0 to 18.0 days.

It is significant that the pack of five wolves had a lower kill rate per wolf than did single wolves and pairs. This is explainable because the ability of wolves to kill deer during early 1969 was much greater than usual (see Mech *et al.*, p. 51). Thus single wolves probably could kill deer just as easily as could packs, but they did not need to share them. This differs markedly from the situation on Isle Royale, where lone wolves usually feed only on moose remains left by packs (Mech 1966a, Jordan *et al.* 1967).

That lone wolves had more of a food surplus than those in the pack is confirmed by the figures on the average number of days that the various wolves fed on kills (table 7). Wolf 1051 spent an average of only 2.2 to 2.4 days feeding at each of his kills, whereas 1059's pack of five spent an average of 5.8 to 7.5 wolf-days at each kill. Further confirmation is found in the fact that even when most wolves were leaving their kills partly uneaten, a pack of 8 to 10 wolves (probably that to which 1057 belonged) was seen completely devouring a kill.

Table 7.—Kill rate of deer by radiotagged wolves and their associates

Wolf number	Wolves	Dates	Wolf-days of data	Kills	Wolf-days per kill[1/]	Wolf-days feeding	Wolf-days feeding per kill
	Number		Number	Number	Mean number	Number	Mean number
1051	1	Nov. 26 to Apr. 3	101	14-16	6.3- 7.2	33- 40	2.2-2.4
1053[2/]	1	Dec. 14 to Mar. 27	75	2- 3	25.0-37.5	9- 18	4.5-6.0
1055	1- 2	Jan. 9 to Mar. 14	61	4- 9	6.7-15.0	13- 25	2.8-3.3
1057	1-13	Jan. 24 to Feb. 28	51	5- 7	7.3-10.2	25- 33	4.7-5.0
1059	5	Jan. 25 to Mar. 14	180	10-13	14.0-18.0	75	5.8-7.5
Summary	22	Nov. 27 to Apr. 3	468	35-48	[3/]9.8-13.4	145-181	[4/]3.8-4.1
		Before Feb. 1	142	7- 9	[5/]15.7-20.3	39- 56	5.1-5.6
		After Jan. 31	326	28-39	8.4-11.6	106-125	3.2-3.8

1/ Kill rate per wolf.
2/ Figures for this animal are so low because she was basically a scavenger.
3/ Average kill rate per wolf for all radiotagged wolves and their associates, derived by dividing total number of wolf-days by total number of kills.
4/ Average number of days that each wolf spent at each kill, derived by dividing total number of wolf-days spent feeding by the total number of kills.
5/ This figure probably is the closest to the actual kill rate during most winters.

Therefore it is probable that the kill rate per wolf for members of the pack of five is much closer to the usual average winter kill rate. It can still be considered higher than the usual winter rate, however, because this pack also was leaving some of its kills partly uneaten.

A reasonable approximation of the average kill rate during most winters would be the rate found for our radiotagged wolves before February 1, because the relations among the wolves, the deer, and the snow during that period were not unlike those of most winters. The average kill rate per wolf before February 1 was estimated at one deer per 15.7 to 20.3 days.

After this period, the rate increased to about one deer per 8.4 to 11.6 days, and an estimated 50 percent of the available food was left uneaten (see Mech *et al.*, page 51). This implies that the kill rate during February and March was about twice as high as usual. On this basis, the usual kill rate would be estimated at one deer per 16.8 to 23.2 days, which checks well with the rate found before February (one deer per 15.7 to 20.3 days). Thus we feel that an estimated kill rate of about one deer per 18 days per wolf is a close approximation of the average kill rate for most winters. This is about 50 percent less than the kill rate of one deer per 4 days estimated by Stenlund (1955) for two packs of three wolves (one deer per 12 days per wolf). However, it compares favorably with the actual kill rate of one deer per wolf per 17.6 days found for a pack of eight wolves in Ontario.[4]

Once the average rate of kill is known, the average food consumption per wolf can be calculated. The average deer (considering both fawns and adults) from the Superior National Forest during winter weighs about 113 pounds (calculated from Erickson *et al.* 1961), and an arbitrary 13 pounds can be deducted from this for inedible portions. This leaves 100 pounds of deer per wolf per 18 days, or 5.6 pounds per wolf per day. This figure is much less than the 10 to 14 pounds estimated consumption rate for wolves feeding on moose on Isle Royale (Mech 1966a). However, much variation can be expected in an animal whose physiology must be adapted to a feast-or-famine existence.

Wolves can be maintained in captivity on 2.5 pounds of meat per day, and large active dogs (*Canis familiaris*) require 3.7 pounds per day, so it is likely that the minimum daily requirement for wolves in the wild is about 4.0 pounds per day (Mech 1970). This figure agrees well with the estimated consumption rate for our study area.

Relative Population Density

Censusing wolves in a 1.5-million-acre study area is a difficult task, and we have no direct information on which to base a population estimate. However, some deductions can be made about the relative population densities in our study area between the period 1948 to 1953 and the period of the present study, 1967 to 1969.

R. A. Rausch (1967a) hypothesized that the frequency of large packs is higher when population density is high, and presented evidence supporting this idea. On this assumption, a comparison of pack-size distributions between various periods can indicate relative population densities between periods. The advantage of this method is that it eliminates the usual type of year-to-year biases in wolf censuses such as might result from differences in precise census route, type of aircraft, skill of observers, and other conditions. Only a difference that would cause a bias in the *size* of the packs seen would be of importance.

Therefore, we tested the difference in size distributions of population units between the 1948-53 study period and the present period (table 1), using a Kolmogorov-Smirnov two-sample test (Siegel 1956). The average "pack" size in the earlier years was 2.8, compared with 4.2 at present; thus pack sizes are significantly larger at present (95 percent level). This indicates that the population density from 1967 to 1969 may have been higher than from 1948 to 1953. This apparent change may be attributable to a reduction in snaring, trapping, and aerial hunting that took place between the two periods as a result of changes in State game regulations.

A similar comparison between our observations from 1967 and those from 1968-69 (table 1) shows no significant difference between these

[4] *Kolenosky, G. B. Wolf movements, activities and predation impact on a wintering deer population in East-Central Ontario. (Manuscript in preparation for publication.)*

years, so it appears that the density of wolves in our area has remained about the same over the period of three winters. This agrees with the results of several other studies summarized by Mech (1970) in which wolf populations unaffected by man have been found to remain relatively stable from year to year.

DISCUSSION AND CONCLUSIONS

The movements, behavior, and ecology of the wolves in our study area during winter are variable, and are influenced considerably by snow conditions. This may explain the fact that in late February 1969 wolves 1051, 1053, and 1055 suddenly extended their travels and range (fig. F-34 and table 4).

However, increased travel may have resulted from other factors. For one thing, the wolves apparently did not need to spend so much time hunting as before. Because of the deep snow, the ability of wolves to capture deer increased, and the animals had a surplus of food. Perhaps under such conditions wolves may use more of their energy for traveling than for hunting.

In this respect it is interesting that 1051 moved right out of his area and traveled into country that presumably was unknown to him. Wolves 1053 and 1055 each ventured into an area that was almost devoid of deer and that even had few moose in it. Without sufficient fat reserves in all these animals, it would seem disadvantageous for them to have made these travels.

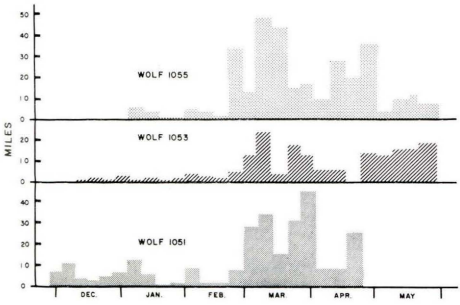

Figure 34.—Net weekly (straight-line) distances traveled by three radiotagged wolves.

Evidently wolves can obtain enough food in much smaller areas than these three animals used after February. Both 1059's pack of five and 1057 lived in relatively small areas throughout the winter and seemed to survive well. Before late February, 1051, 1053, and 1055 did also. Thus some factor other than food must have influenced the movements of these three animals from late February through April.

The fact that the increased movement began during the breeding season makes one suspect a relationship between the two. One possibility is that the factors increasing the hormonal flow associated with breeding in adults stimulate a hormone output in immature or subordinate individuals that causes an increase in their movements. An alternative is that the breeding behavior of resident packs involves the beginning of, or an increase in, aggression toward neighboring nonmembers. This might force the lone animals to shift about over large areas in avoidance of such aggression.

Whatever the cause of the changes in movements of these animals, the fact that the pack used a much smaller area than any of the lone wolves may be of central importance in trying to understand the organization of the wolf population. The following pieces of information are also pertinent to such an understanding: (1) the pack, which can be presumed to include a breeding pair (Mech 1970), chased other wolves in its area; (2) the lone wolves, which apparently did not breed, were tolerant of, or indifferent to, other lone wolves in their areas; (3) the ranges of the lone wolves overlapped considerably (fig. 35); (4) the lone wolves seemed to avoid certain large areas that one might logically think would have been visited by them (fig. 35); and (5) packs of wolves were sometimes observed in these large areas (fig. 35).

From the above information it can be hypothesized that the wolf population consists basically of groups of breeding packs defending territories of limited size, with lone wolves and other nonbreeding population units that are tolerant of each other shifting about in much larger nonexclusive areas among these territories. The information from Isle Royale (Mech 1966a, Jordan

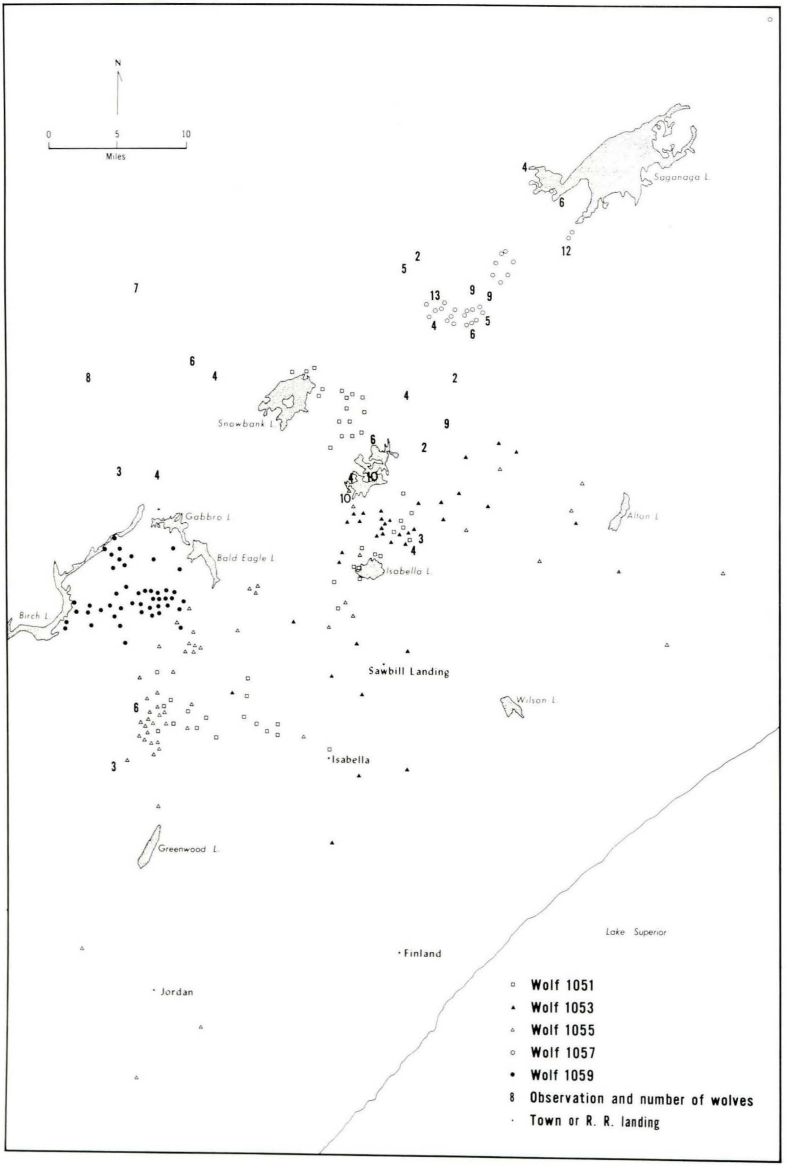

Figure 35.—Locations of all radiotagged wolves and unmarked packs observed during winter 1968-69, *except dispersal of* 1051 *out of the study area. Only selected lakes shown.*

et al. 1967) is consistent with this idea, but the area of that island (210 square miles) is too small to allow untested extrapolations to be made about spacing in much larger wolf populations. Data from Algonquin Park, Ontario (Pimlott *et al.* 1969) also strongly suggest this hypothesis. However, the packs studied there could not be identified with certainty, and little information was obtained about nonbreeding population units.

To test the proposed hypothesis with certainty, a larger number of identifiable breeding and nonbreeding population units from the same general area must be followed during at least one winter. This will be the main objective of our next study.

SUMMARY

During the winters of 1966-67, 1967-68, and 1968-69, aerial observations of timber wolves (*Canis lupus*) were made in the Superior National Forest in northeastern Minnesota, where the primary prey is white-tailed deer (*Odocoileus virginianus*). In 480 hours of flying during the study, 77 sightings involving 323 wolves were made. In addition, during 1968-69, five radiotagged wolves and their associates were tracked via receivers in aircraft for a total of 570 "wolf-days." Visual observations were made during 65 percent of the times the wolves were located from December through April.

The average size of each population unit (including single wolves, pairs, and packs) observed was 4.2, although packs of as many as 13 wolves were sighted. Radiotagged wolves spent most of their daylight hours resting during winter, and when traveling, hunting or feeding during the day, tended to do so before 11:00 a.m. and after 3:00 p.m.

Considerable variation was discovered in the movement patterns of individual wolves, with straight line distances between consecutive daily locations ranging from 0.0 to 12.8 miles, and between weekly locations, 0.0 to 49.0 miles. A pack of five wolves used a range about 43 square miles in extent, whereas lone wolves covered areas many times this size. One animal in an apparent dispersal was tracked a straight line distance of 129 miles between extreme points.

A reddish male wolf was the leader of the pack of five and led two observed chases after alien wolves in the pack's territory. This animal was also most active during scent marking by the pack. Lone wolves were apparently indifferent to other wolves, and thus exclusive areas, or territories, were not observed among lone wolves.

Hunts involving a total of seven deer were observed and described, and two successful attacks on deer were interpreted from tracks in the snow. Wolves generally consumed all the flesh and much of the hair and bones from kills, except during February and March 1969 when extreme snow conditions increased the vulnerability of deer to an unusual degree. At that time kills were found that were partly or totally uneaten. The kill rate by radiotagged wolves and associates during the winter of 1968-69, based on 468 wolf-days of data, varied from one deer per 6.3 days to one per 37.5 days per wolf, with the average being one deer per 10 to 13 days. The rate was much lower per wolf for members of the pack of five than for lone wolves, and much lower before February 1, 1969, than after. The average rate of kill during more usual winters was estimated to be about one deer per 18 days. This is a consumption rate of about 5.6 pounds of deer per wolf per day.

Indirect evidence based on comparisons of pack-size distributions for different periods indicates that the wolf density in the study area may have increased since 1953, but that it has remained the same from 1967 to 1969.

On the basis of data presented in this paper, the following hypothesis about the organization of the wolf population studied is proposed: The wolf population consists basically of groups of breeding packs defending territories of limited size, with lone wolves and other nonbreeding population units, tolerant of each other, shifting about in much larger nonexclusive areas among these territories.

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This report was reviewed by the following biologists: Mr. G. B. Kolenosky, Dr. P. A. Jordan, Mr. M. H. Stenlund, and Dr. D. L. Allen.

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AN ANALYSIS OF THE AGE, SEX, AND CONDITION OF DEER KILLED BY WOLVES IN NORTHEASTERN MINNESOTA

L. David Mech and L. D. Frenzel, Jr.

The selective effect of predation on prey populations is of significance in studies of evolution and population dynamics. Selective predation can be an important agent in the process of natural selection, and it influences the extent to which predators limit the numbers of their prey.

One of the predators most commonly chosen for investigating the selective effect upon prey is the wolf (*Canis lupus*). Because animals preyed upon by wolves generally are large, their remains can be more easily located and examined. It already has been established that in most areas wolves kill primarily young, old, and other inferior members of such prey populations as Dall sheep (*Ovis dalli*), moose (*Alces alces*), caribou (*Rangifer tarandus*), bison (*Bison bison*), and musk-oxen (*Ovibos moschatus*); evidence for this generalization has been summarized by Mech (1970).

However, only recently has it been shown that this generalization may extend to predation on the smallest hoofed prey of the wolf in North America, the white-tailed deer (*Odocoileus virginianus*). Pimlott *et al.* (1969) demonstrated a difference between the age structure of 331 deer killed by wolves during winter in Algonquin Park, Ontario, and 275 deer assumed to represent the actual population in the same area. Whereas only 13 percent of the deer from the population at large were estimated to be more than 5 years old, 58 percent of the wolf-kills were in this age category.

We employed a similar analysis for deer killed by wolves in northeastern Minnesota, but used a more refined aging technique and included comparisons of the age and sex structures of various subsamples of wolf-kills. Whereas the Ontario research involved a prey population unhunted by man, our work was carried out on both a hunted population and on one relatively unhunted. Further comparisons were made between deer killed during periods of normal snow conditions and those taken during unusually high snow accumulations. The incidence of various abnormalities in wolf-killed deer was also com-

pared with that in hunter-killed animals.

The study was carried out in the Superior National Forest in northern St. Louis, Lake, and Cook Counties of northeastern Minnesota (fig. 1), in conjunction with other aspects of wolf research (see Mech *et al.* p. 1).

METHODS

The investigation began in February 1966 and continued through March 1969; the basic objective was to examine as many wolf-killed deer as possible and compare their ages, sex, and condition with a large sample of deer from the population at large in the same area. Wolf-kills were examined only during December through March when they could be found from the air. Aircraft ranging in size from an Aeronca champ to a Cessna 206 were used to fly over frozen lakes at altitudes up to 2,000 feet to locate wolves (fig. 2), wolf tracks, or kills (fig. 3). We often discovered kills by tracking a wolf pack.

During the winter of 1968-69 this method of finding kills was supplemented by radiotracking five wolves and their associates via aircraft (see Mech *et al.*, p. 1). The latter technique resulted in increased discovery of inland kills.

A deer carcass was judged killed by wolves if the death had been recent, if tracks or other sign indicated that wolves had fed upon it, and if no other possible cause of death was discovered. Carcasses fed on by wolves but not clearly identifiable as kills were labeled "probable" wolf-kills. Although the cause of death of the specimens in this latter category could not be deter-

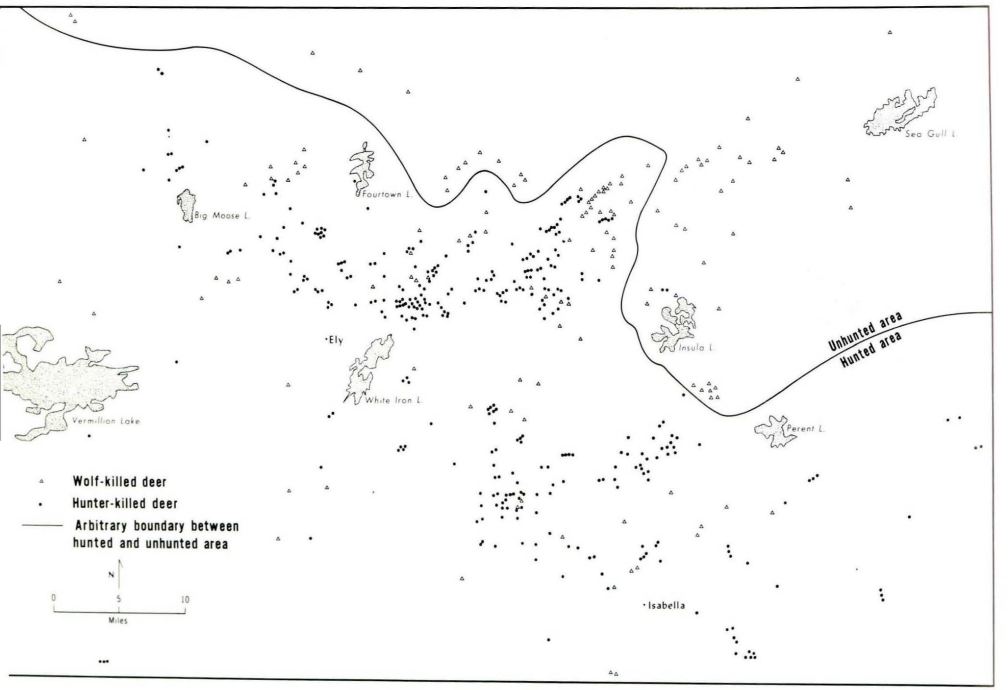

Figure 1.—The study area showing locations where wolf-killed and hunter-killed deer were taken. Line arbitrarily separates the hunted area from the wilderness area.

mined with certainty, there was no reason to believe other agents were involved.

In addition to the wolf-kills examined by project personnel, data and lower jaws from deer judged killed by wolves were contributed by other biologists, game wardens, forest rangers, and others whose competence was known. Nevertheless, if certain identification of carcasses as wolf-kills was not possible, the data were relegated to the "probable" wolf-kill category.

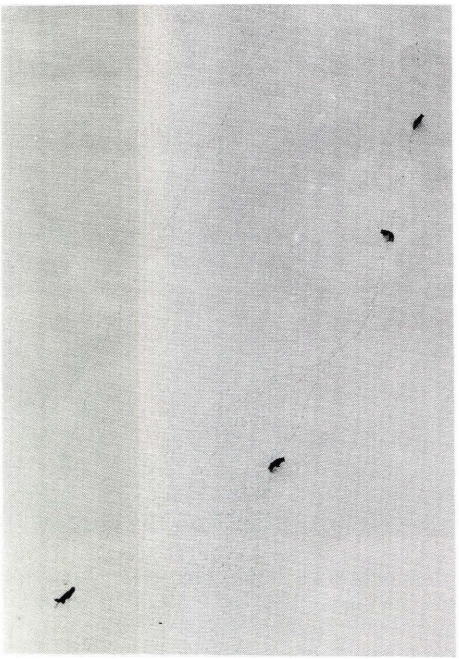

Figure 2.—Wolves were located from the air, usually on frozen lakes. (Photo courtesy of L. D. Mech.)

Whenever possible, kills discovered from the air were examined on the ground (fig. 4). Often only skeletal parts remained, but soft parts were also examined when available. Femur marrow, heart, lungs, liver, kidneys, repreductive tracts, and omenta were usually inspected in the field for fat, parasites, and abnormalities, and the degree of subcutaneous back fat was also noted. Hoofs and lower legs were checked, and those showing pathological conditions or abnormalities were collected and examined by the Veterinary Diagnostic Laboratory of the University of Minnesota. All lower jaws found were collected, aged, and examined for dental abnormalities and pathological conditions.

In November 1967 and 1968 hunter-check stations were operated on the study area (fig. 5), and deer bagged by hunters were field-checked for age (Severinghaus 1949) and hoof abnormalities. As many lower jaws as possible were collected from field-checked deer and other deer killed in the area for age determination and examination for abnormal dentition.

An assumption was made that the age structure and incidence of abnormalities in the sample of hunter-killed deer would be *reasonably representative* of those in the population at large, an assumption also implicit in a similar comparison made by Pimlott *et al.* (1969). In this respect, the following statements by Maguire and Severinghaus (1954, p. 109) about deer in New York State are pertinent: "It may be concluded that, considering the open season as a whole, wariness does not significantly distort the age composition of the [deer] kill in relation to that of the corresponding wild population, except possibly for buck seasons of only 1 or 2 days duration . . . A reliable appraisal of the age composition of the kill by hunting may be obtained through the operation of roadside checking stations." However, in critically reviewing the present paper Severinghaus stated that in States such as Minnesota, with fewer hunters and higher hunter success rates, age compositions of deer from checking stations may not be the same as those of wild populations. Reviewers Peek and Downing also made similar comments.

Nevertheless, for our comparison with wolf-killed deer it is not necessary that the hunter-kill age structure be exactly representative of the age structure of the actual deer population. All that is required is that there be reasonable agreement between the two. The hunting regulations in our study area allow a 9-day period of taking deer of any age or sex, and a single hunter may legally shoot as many deer as he and his party or associates have permits for. Thus there is no reason for selective hunting, and

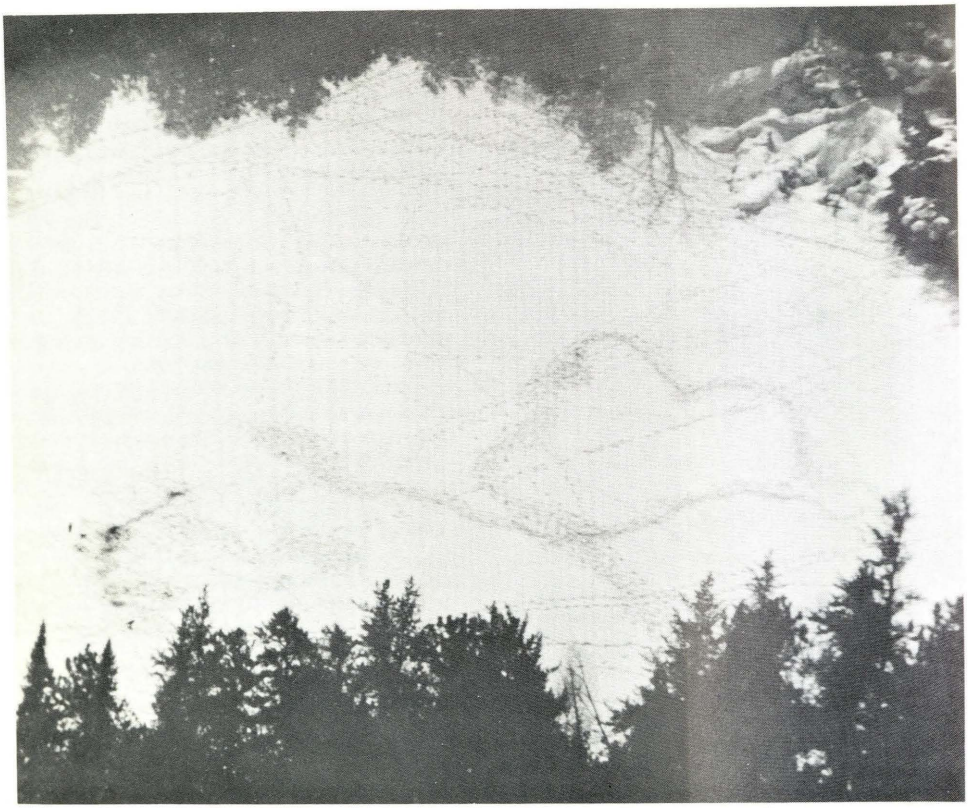

Figure 3.—Wolf-kills were easily spotted from aircraft. (Photo courtesy of L. D. Mech.)

we feel confident that the age structure of the hunter-kill in our study area does basically represent that of the deer herd at large.

Two laboratory techniques were used for determining the ages of deer from the lower jaws or mandibles – a tooth replacement and wear technique (Severinghaus 1949) and an incisor-sectioning method (Gilbert 1966). The tooth-wear technique requires only the molariform teeth but it is more subjective and inaccurate, particularly in older deer (Ryel *et al.* 1961). Incisor sectioning requires only incisors and appears to be much more accurate.

However, because the incisors had been lost from many of the wolf-kills, and because the tooth-wear technique was used at checking stations, both methods were applied in the laboratory. Mr. David W. Kuehn (1970) sectioned and aged the incisors. Fortunately there was a sufficiently large sample of mandibles with molariform teeth and incisors from both wolf-killed and hunter-killed deer to enable us to devise a table showing the actual ages (based on incisor-sectioning) of each of the jaws assigned to various tooth-wear classes. This table was then used to distribute the ages of specimens that con-

Figure 4.—As many wolf-killed deer as possible were examined from the ground. (Photo courtesy of L. D. Mech.)

tained only molariform teeth. For example, because it was found that 37 percent of the jaws aged 4½ years old by tooth wear were actually 5½ years old, we assigned 37 percent of the incisorless jaws aged 4½ by tooth wear to the 5½-year category. Similarly, another conversion chart comparing field age determinations of hunter-killed deer with ages based on incisor sectioning of the same jaws was employed to distribute the ages of field-aged, hunter-killed deer for which jaws or incisors could not be collected.

RESULTS

We flew a total of 480 hours during this and related research, mainly during January through March 1967 and December 1968 through March 1969; about one-third of this time was devoted primarily to searching for kills. Jaws were examined from 93 wolf-kills and 49 probable wolf-kills.

Hunter-check stations yielded information from 335 deer (fig. 6), and data on 98 addi-

Figure 5.—Information about hunter-killed deer in the study area was obtained through hunter-check stations. (Photo courtesy of L. D. Frenzel.)

tional hunter-killed deer were contributed by other hunters. Incisors were collected from 82 of 214 hunter-killed deer checked that were older than yearlings; comparisons were then made between ages of the deer based on incisor sectioning and those based on field checks using the wear method. Similarly, incisors were sectioned from 195 wolf-killed and hunter-killed deer older than yearlings that had been aged by the tooth-wear method in the laboratory, so that these two methods could be compared

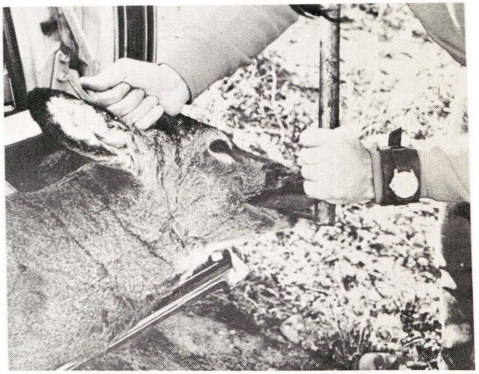

Figure 6.—All hunter-killed deer examined were checked for age. (Photo courtesy of L. D. Frenzel.)

(Kuehn 1970). (Note: incisor-sectioning is unnecessary for fawns and yearlings because animals of these ages can be aged objectively by the progress of tooth replacement.)

Because age or sex distributions might differ in the various subsamples of deer examined during this study, these parameters were compared in subsamples of both wolf-kills and hunter-kills (table 1). No significant differences were found in the age or sex structures between the known wolf-kills and "probable" wolf-kills, so these subsamples were pooled and considered wolf-kills for all subsequent comparisons.

Three significant differences in sex ratio were found among the subsamples of wolf-kills: (1) wolves killed more female fawns than male fawns, but more male adults than female adults (table 2); (2) more of the adults killed in the hunted area were females, while in the wildnerness more males were taken (table 3); and (3) after January 1969, when snow was unusually deep, 57 percent of the deer killed were females, compared with only 38 percent before this date.

Table 2.—Sex ratios of hunter-killed deer and wolf-killed deer from northeastern Minnesota

Age	Hunter-killed deer			Wolf-killed deer		
	Number	Percent male	Percent female	Number	Percent male	Percent female
Fawns	108	50	50	22	41	59
Adults	315	68	32	105	54	46

In the comparisons of the subsamples of hunter-kills, the only statistically significant difference found was that the adult subsample had a higher proportion of males than the fawn subsample. No significant difference was found in the age structures of the subsamples, so these were all pooled into a sample of 433 hunter-kills for comparison with the wolf-kills. For the same reason, the entire sample of 142 wolf-killed deer was used for a comparison with the hunter-killed sample.

Wolf-killed deer in our sample, with an average age of 4.7 years, were significantly older (99 percent level) than hunter-killed deer, with an

Table 1.—Results of statistical comparisons between various samples of deer kills from northeastern Minnesota

Sample size	Sample description	VS	Sample size	Sample description	Results of comparisons: Age structures[1]	Results of comparisons: Sex ratios[2]	Direction of difference
	Wolf-kills:[3]			Wolf-kills:[3]			
93	Known		49	Probable	Nonsig.[4]	Nonsig.	--
42	Jan.-Mar. 1967		83	Dec. 1968-Mar. 1969	Nonsig.	Nonsig.	--
66	Male		61	Female	Nonsig.	--	--
50	Wilderness area		92	Hunted area	Nonsig.	Nonsig.	
41	Adult, wilderness		64	Adult, hunted area	--	Sig., 99 percent	More females in hunted area
96	Lakes[5]		32	Inland	Nonsig.[6]	Nonsig.	--
66	Before Feb. 1969		77	After Jan. 1969	Nonsig.[7]	Sig., 95 percent	More females after Jan.
105	Adults		22	Fawns	--	Sig., 95 percent	More female fawns
	Hunter-kills:			Hunter-kills:			
110	Field aged, 1967		225	Field aged, 1968	Nonsig.	Nonsig.	--
335	Field aged		98	Lab. aged	Nonsig.	Nonsig.	--
132	Lab. aged, males		79	Lab. aged, females	Nonsig.	--	--
89	Field aged, fawns		246	Field aged, adults	--	Sig., 95 percent	More male adults
433	Hunter-kills		142	Wolf-kills	Sig., 99 percent	--	Older deer in wolf-kill
321	Hunter-kills excluding fawns		118	Wolf-kills excluding fawns	Sig., 99 percent	--	Older deer in wolf-kill

1/ Kolmogorov-Smirnov two-sample test (Siegel 1956).
2/ χ^2 test (Downie and Heath 1959).
3/ Because test showed no significant differences in age or sex structure between sample of known wolf-kills and probable wolf-kills, these were combined for all subsequent tests and the pooled sample considered "wolf-kills."
4/ At 95 percent level or greater. (NOTE: Lack of a significant difference does not prove that no difference exists. Rather, it means only that the available evidence does not allow the positive conclusion that a difference does exist.)
5/ Wolf-kills found on lakes were compared with those located inland because of the possibility that kills on lakes may not be representative of kills in general.
6/ Sample too small for test, but no apparent difference.
7/ No significant difference in entire age structures. However, when the percentage of yearlings is compared between the two groups, the difference is almost significant at the 95 percent level.

Table 3.—Sex ratios of wolf-killed deer from wilderness areas and from hunted areas

Age	Wilderness area			Hunted area			Total		
	Number	Percent male	Percent female	Number	Percent male	Percent female	Number	Percent male	Percent female
Fawns	4	0	100	18	50	50	22	41	59
Adults	41	71	29	64	44	56	105	56	44

average age of 2.6 years. For example, deer 5 years of age and older made up 48 percent of the wolf-kills but only 10 percent of the hunter-kills (table 4). The oldest hunter-killed deer in our sample was 9½ years old, but the oldest wolf-killed deer was 14½ (fig. 7).

Because of a possible bias against fawns in the method of collecting data from wolf-kills (to be discussed later), the age structure of the sample of wolf-kills excluding fawns was tested against that of the sample of hunter-kills excluding fawns. The result once again was a highly significant difference between these two age structures (table 1).

As an additional test of the degree to which the age structure of the wolf-killed deer might differ from that of the actual population, we compared our wolf-kill age structure with the age structure of a hypothetical deer population. This was considered advisable just in case the hunter-kill data were poorly representative of the age structure of the actual deer herd. Several hypothetical age structures were constructed and compared according to advice from Downing.[1] In all cases, the comparisons produced the same basic results as the tests with the hunter-killed sample. An example of one comparison is given in figure 7.

A further result obtained by aging the wolf-killed deer pertained to the young individuals killed. The deciduous first incisors of fawns and the decidous premolars of yearlings are usually replaced with permanent teeth by December (Severinghaus 1949). Of 24 wolf-killed fawns examined, however, three (13 percent) taken during January, February, and March had not yet replaced their deciduous first incisors. Of the 13 yearlings found during this same period, nine (70 percent) had failed to replace their deciduous premolars, and two (15 percent) had just replaced them (one deer killed in February and one killed in March).

Mandibles from the 142 wolf-killed deer and 259 hunter-killed deer were examined closely for

[1] *R. L. Downing. Personal correspondence to L. D. Mech, October 2, 1969.*

Table 4.—Age and sex distribution of deer killed by wolves and hunters in northeastern Minnesota

Age (years)	Wolf-killed deer					Hunter-killed deer				
	Number of:				Percent	Number of:				Percent
	Males	Females	Unknown	Total		Males	Females	Unknown	Total	
Fawns	9	13	2	24	17	54	54	4	112	26
1+	5	7	1	13	9	63	26	1	90	21
2+	3	8	5	16	11	42	19	2	63	15
3+	2	4	2	8	6	47	16	1	64	15
4+	6	3	4	13	9	32	22	1	55	13
5+	12	9	--	21	15	15	12	1	28	6
6+	9	2	1	12	8	3	--	--	3	--
7+	12	4	--	16	11	7	4	--	11	3
8+	4	2	--	6	4	5	1	--	6	1
9+	4	2	--	6	4	1	--	--	1	--
10+	--	3	--	3	2	--	--	--	--	--
11+	--	1	--	1		--	--	--	--	--
12+	--	--	--	--	4	--	--	--	--	--
13+	--	1	--	1		--	--	--	--	--
14+	--	2	--	2		--	--	--	--	--
Total	66	61	15	142	100	269	154	10	433	100

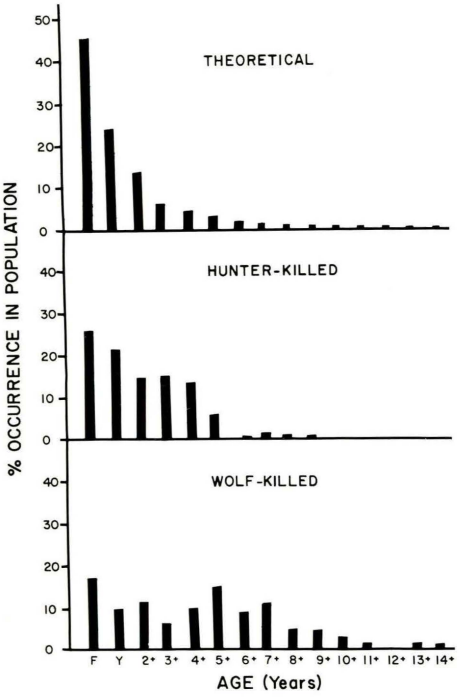

Figure 7.—Comparison between the age structures of deer killed by wolves, deer killed by hunters, and a theoretical population from the same general area of northeastern Minnesota.

abnormal dentition (table 5, figs. 8-10) (Mech *et al.* 1970) and pathological conditions (table 6), and the lower limbs of 75 wolf-kills and 126 hunter-kills were also checked for abnormalities and pathology (table 7, fig. 11). Statistical comparison showed that the incidence of each condition was significantly higher in the sample from wolf-killed deer (table 8).

Jaw necrosis found in our specimens was similar to that described by Murie (1944) for Dall sheep and Mech (1966a) for moose. Generally animals with this condition are old, and ours were no exception.

The following organs were excised from wolf-killed deer end examined grossly in the field for parasites and abnormalities (fig. 12): lungs (six

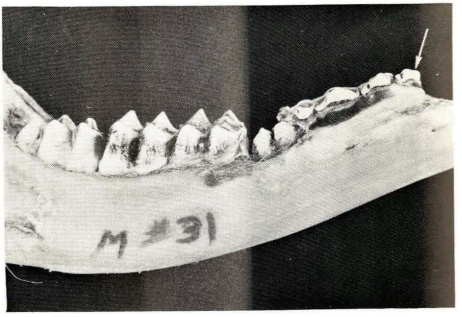

Figure 8.—Deciduous first premolar (arrow), usually not present in deer, was found in specimen M-31.

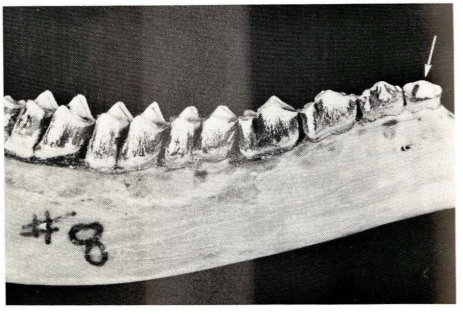

Figure 9.—A permanent first premolar (arrow) was discoverd in M-8.

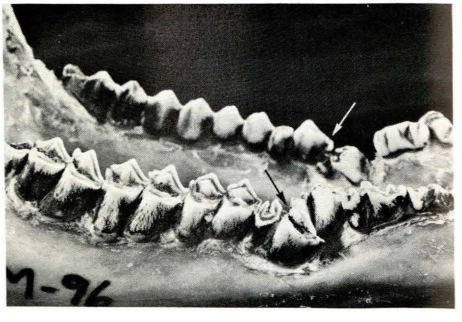

Figure 10.—An extra set of fourth premolars (arrows) occurred in specimens M-96.

Table 5.—Abnormalities in the mandibular dentition of deer from the Superior National Forest, Minnesota

Specimen number	Sex	Age[1]	Cause of death	Side of jaw[2]	Abnormality
		Years			
M-8	F	3+	Wolves	Right	P_1 present (fig. 9)
				Left	Normal; no P_1 present outside or inside jaw
M-31	F	17 mon.	Wolves	Both	Deciduous P_1 present (fig. 8) and permanent P_1 present inside left ramus; right side not examined internally
M-45	M	4+	Wolves	Right	P_2 rotated 90°
				Left	P_2 absent
M-52	M	4+	Wolves	Right	P_2 absent
				Left	Normal
M-96	F	2+	Hunters	Right	2 permanent P_4s present; both crooked in orientation (fig. 10)
				Left	P_2 diagonal; P_3 normal; P_4 below gumline, pointed posteriorly and wedged against M_1; appears to have pushed out original P_4 (fig. 10)
M-117	M	5+	Hunters	Right	Third column of M_3 reduced
M-191	M	4+	Wolves	Right	Third column of M_3 absent although rudimentary root present
				Left	Third column of M_3 much reduced, peg-like, and almost separate
M-225	--	4+	Wolves	Right	P_2 absent
				Left	P_2 situated diagonally
M-234	F	5+	Wolves	Right	Third column of M_3 reduced
M-254	M	2+	Hunters	Right	P_2 slightly crooked in orientation
				Left	P_2 slanting posteriorly and crowding P_3
M-272	M	5+	Hunters	Right	Third column of M_3 reduced, peg-like, and almost separate
				Left	Third column of M_3 peg-like and separated from second column by 4 mm.
M-296	F	5+	Wolves	Right	Normal
				Left	Extra permanent P_4 crowding original P_4; much like M-96
M-369	M	3+	Hunters	Right	Permanent P_2 still not emerged but appears to be wedged against root of P_3

1/ Based on incisor sectioning method of Gilbert (1966) except that underlined figures are based on tooth replacement or wear (Severinghaus 1949).
2/ Where only one side is listed, the other was not available.

Table 6.—Pathological conditions in the lower jaws of deer killed by wolves or hunters[1]

Specimen number	Sex	Age	Cause of death	Approximate date of death	Condition
		Years			
M-70	M	6½	Wolves	Feb. 1968	Lump in left side of mandible near M_1 and M_2
M-192	M	7½	Wolves	Jan. 1969	Large lump in left diastema apparently from healed fracture
M-206	M	8½	Wolves	Jan. 1969	Light necrosis around base of teeth
M-218	M	3½	Wolves	Feb. 1969	Large lump in left diastema apparently from healed fracture
M-228	F	11½	Wolves	Mar. 1969	Heavy necrosis around molars and extending into bone; half of each M_3 destroyed, both roots and crown
M-236	F	14½	Wolves	Feb. 1969	Light necrosis around base of teeth
M-402	F	10½	Hunters	Nov. 1968	Heavy necrosis and lumps on both sides of mandible

1/ Not including dental abnormalities, which are described in table 5.

animals, normal); heart (seven animals, normal); liver (four animals, one small unidentified tapeworm cyst). Twin fetuses were found in each of two adult does examined.

Twelve deer were checked for body fat in one or all of the following areas: back (subcutaneous), kidneys, heart, omenta. Of these animals, seven had large amounts of fat, but five were almost depleted of fat from these stores. These five were all killed in February or March 1969; three were fawns, and two were yearlings that had not yet shed their deciduous premolars.

Of 69 animals examined for femur marrow condition, two had fat-depleted marrow. One was a fawn killed in March 1969 that had not shed its deciduous first incisors, and the other was a 5½-year-old buck killed in February 1966.

A fawn and a yearling that had died in February 1969 from unknown causes also had fat-depleted marrow. These animals might have been killed by wolves, for wolves had fed on them. However, they could have died from malnutrition and been eaten as carrion.

Table 7.—Pathological conditions in the lower limbs of deer killed by wolves or hunters

Specimen number	Sex	Age	Cause of death	Condition
		Years		
M-28	M	5½	Wolves	Right hind foot: "Old healed ankylosis of the pastern joint ... a spontaneously healed bacterial arthritis with the destroyed joint cavity filled in by solid bone. This deer probably had defective gait"[1/] (fig. 14).
M-29	F	5½	Wolves	Front foot: "A 3x4x5 cm. fibrous mass in the subcutis about the digital flexor tendon on the volar surface of the metacarpus. The surface was denuded, ulcerated, and superficially infected by surface bacteria. ... Probably did detract from the animal's speed of flight"[1/] (fig. 15).
M-37	F	7½	Wolves	Hind foot: "Probable that the lesion was at one time an active bacterial bone marrow infection that had eventually fistulated to the skin. ... Regional tendons and their sheaths were also present among this inflammation and scarring, and it would be fair to assume that the animal's agility was impaired to some extent."[1/]
M-115	M	4½	Hunter	Right front hoof: Broken at tip.
M-196	F	4½	Wolves	Left front foot: "Two severe transverse lacerations on the volar surface. Each was approximately 4 cm. in length. One was located at the margin of the heel, and the other was located several cm. proximad. The more proximal wound had severed the flexon tendons, and the consequent uselessness of the limb was suggested by the splayed toes, the unmarred hoof wall and unworn soles"[2/] (fig. 16).
M-227	M	9½	Wolves	Left hind leg: "A diffuse swelling of the distal metatarsal bone, the surface of which was studded with small osteophytic spicules. The major flexor and extensor tendons were forced to assume a convex course over the summits of the dorsal and plantar surfaces of the defect, but the tendon sheaths were clean and the normal wear on soles of the involved toes suggested that functional deficit and pain were probably minimal. ... quite certainly a callus from previous fracture"[2/] (fig. 17).

1/ D. M. Barnes. Personal correspondence to L. D. Mech, April 11, 1967.
2/ D. M. Barnes. Undated laboratory report transmitted to L. D. Mech in 1969.

DISCUSSION AND CONCLUSIONS

It has been established that wolves hunting Dall sheep (Murie 1944), caribou (Crisler 1956), moose (Mech 1966a), and other species usually have a low percentage of success. In the case of a pack of 15 wolves hunting moose on Isle Royale during winter, only 4.6 percent of all the moose detected by the pack were killed; considering only the moose that the wolves caught up to or held at bay, the kill rate was 7.6 percent (Mech 1966a).

Figure 11.—The jaws and legs of kills were inspected closely for abnormalities. (Photo courtesy of L. D. Frenzel.)

What little evidence there is about wolves hunting deer indicates that the success rate is also low with this prey species, at least in winter. The senior author has now observed a total of 14 deer being chased by wolves in northeastern Minnesota, mostly by packs of five, seven or eight wolves (Mech 1966b, and see Mech *et al.*, p. 1). In only one case (6.7 percent) did the wolves (a pair) succeed in catching their prey.

Low hunting success rates imply that the circumstances influencing hunts are seldom favorable enough, or the prey animals encountered are seldom vulnerable enough for the wolves to succeed. When the evidence cited earlier that most wolf-killed animals are inferior members of their populations is considered, the most cogent explanation for the low hunting success of wolves is that relatively few prey animals are vulnerable.

Table 8.—Incidence of various abnormalities and pathological conditions in wolf-killed deer compared with that in hunter-killed deer

Condition	Wolf-kills			Hunter-kills			Level of significance
	Deer in sample	Deer with condition		Deer in sample	Deer with condition		
	Number	Number	Percent	Number	Number	Percent	Percent
Dental abnormalities	142	8	5.6	259	5	1.9	2/90
Jaw necrosis, lumps, or fractures 1/	142	6	4.2	259	1	0.4	2/95
Pathology of lower limbs	75	5	6.7	126	1	0.8	95

1/ Two mandibles from wolf-killed deer had large lumps from healed fractures in the region of the diastemas.

2/ If all dental and jaw abnormalities are pooled, the difference between the incidence in the wolf-kill sample (9.8 percent) and that in the hunter-kill (2.3 percent) is significant at the 99 percent level.

Figure 12.—When internal organs were present in kills, they were examined in the field. (Photo courtesy of L. D. Mech.)

Age Structure

Our data strongly indicate that in northeastern Minnesota wolves prey much more heavily on the older members of the deer population, at least during winter (fig. 7). Substantial vulnerability to wolves seems to begin at about the age of 5 years (fig. 13), because the percentage of wolf-killed deer in each year class increases from 9 percent for 4½-year-old animals to 15 percent for 5½-year-olds (table 4). Indeed, 48 percent of the wolf-kills were aged 5½ and over, which compares favorably with the Ontario figure of 58 percent for these age classes (Pimlott *et al.* 1969).

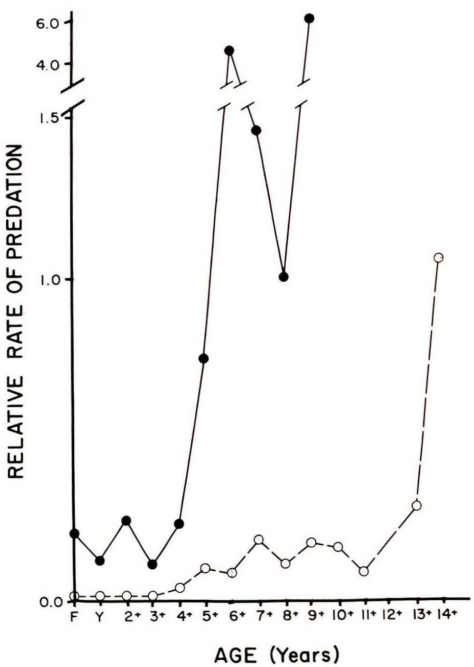

Figure 13.—Relative rates of predation on deer of various ages, based on comparisons of the ages of wolf-killed deer with those of a theoretical population (dashed line) and those of the hunter-killed population. See figure 7.

These figures assume added significance when compared with a sample of deer killed by hunters in the same general area (fig. 1). Only 10 percent of the hunter-killed deer were 5½ years old or older, and the percent killed in each year class dropped off suddenly from 13 percent aged 4½ to 6 percent aged 5½. If the age structure of the hunter-kill sample is reasonably representative of the age structure of the population at large, the wolf-kill data show that wolf predation in our study area during winter has a definite selective effect on the deer population.

There is no direct way of knowing that the age structure of the hunter-killed deer represents the age structure of the deer population at large. However, sampling hunter-kills is the most practical means available for gaining an index to the age structure of the existing herd. Further, there are three indirect pieces of evidence indicating that the hunter-kill sample represents the actual age structure of the population, just as Maguire and Severinghaus (1954) found in New York. First, our sample has the basic theoretical form expected of a stable deer herd; i.e., the youngest year class contained the most members, and each older cohort included fewer (fig. 7). Second, the age structure of our sample has the same form as most other deer age structures from widely diverse areas, (Ontario, Pimlott *et al.* 1969; southern Minnesota, Erickson *et al.* 1961; Massachusetts, Shaw 1951). Third, there is no reason to believe that in our area rifle hunting is especially selective for any particular age classes. In talking with large numbers of hunters, we have learned that most shoot at any and all deer they happen to see.

Even if the age structure of the hunter-kill sample did not approximate that of the actual herd, the comparison of the wolf-kill with the theoretical population dictates the same conclusion: the rate of kill of older deer by wolves was several times greater than that of younger deer, excluding fawns (fig. 13). In any case, if the actual deer population in our study area had an age structure similar to that of our sample of wolf-kills (which would be the only age structure that would contradict our conclusion), its numbers would be declining by orders of magnitude each year, and there would now be only a remnant population. Such obviously is not the case.

The only other question that might arise from a comparison of the age structure of our wolf-killed deer with that of the hunter-killed deer concerns the area from which each sample was taken. Fifty of our wolf-kills came from a region almost inaccessible to hunters (fig. 1). However, the other 92 came from the same general area as the hunter-kills. Nevertheless, there was no statistically significant difference in age structure between the wolf-kills from the wilderness versus those from the hunted area (table 1). This fact also suggests that the human hunting in the area is relatively light and has little effect on the age structure of the deer population in the area.

Wolves may also be taking a disproportionately high number of fawns, although our data do not show this. Nevertheless, there may be a bias against fawns in our method. It is not unusual to discover the remains of a wolf-killed deer so completely eaten that there is no indication left of the animal's age. Because fawns often are only about half the size of adult deer, and their skeletons have not yet completely ossified, the chances are better that fawns will be more completely eaten. Pimlott *et al.* (1969) also recognized this possible bias, although their data did indicate that wolves were killing a higher percentage of fawns than occurred in the population.

Our study does support the other conclusion of Pimlott *et al.* (1969), based on a study of 331 kills, that wolf predation on deer during winter shows a definite selection for older animals. It does not agree with the tentative conclusion of Stenlund (1955) that wolves in the Superior National Forest do not prey disproportionately on old deer. However, Stenlund's conclusion was based on 36 kills and on the assumption that only deer at least 7 years old were "old." Deer 5 years old and older composed 33 percent of Stenlund's sample, a figure considerably higher than the 10 percent in these age classes in our hunter-kill sample (table 4). Thus Stenlund's data do not contradict our conclusion.

The age of 5 years seems to be the beginning of the period of vulnerability for adult deer. Although 5 years might not seem especially old, there are two aspects of significance concerning deer of this age and older. First, they are in the second half of the life span for most members

of the species, and their alertness and ability to bolt quickly away might be expected to decline. It is of interest in this regard that Klein and Olson (1960, p. 87) believed 5 years of age to be "the upper limit of physiological efficiency" of black-tailed deer (*Odocoileus hemionus*) in Alaska. Second, up to the age of at least 4½ years, and perhaps beyond, the apparent weight-load-on-track of deer increases with age (Kelsall 1969). Thus older deer would sink farther into the snow than younger ones, and their escape might be slowed and hindered more. For further discussion of the effect of snow on the vulnerability of deer, see Mech *et al.* (p. 51).

Sex Ratio

Statistical tests comparing a number of subsamples of both wolf-killed deer and hunter-killed deer showed a series of significantly different sex ratios (tables 1-3). The ratio of males to females in the fawn cohort of the hunter-kill, which is probably the most representative of the actual fawn sex ratio, was even (table 2). With wolf-kills, however, a significantly higher percentage of females was taken in the fawn subsample (59 percent) than in the adult subsample (46 percent). These results compare favorably with those of Stenlund (1955), who found that from 1948 to 1953 in the same area as the present study 68 percent of 19 sexable fawn wolf-kills were females and 44 percent of 63 sexable adult wolf-kills were females.

If the sex ratio of fawns began even, and more females than males were killed by wolves, then a higher proportion of males would be left in the adult population, unless some other mortality factor kills more male fawns. Thus it is not surprising that in the wildnerness area, where little or no hunting is done, the sex ratio of wolf-kills in the adult cohort is significantly heavy toward males (71 percent : 29 percent). This was also true of the wolf-kills in Algonquin Provincial Park, where males made up 57 percent of the total sexable wolf-kill (Pimlott *et al.* 1969). The latter figure may even have been higher if calculated for adults alone, for a preponderance of female fawns in the Algonquin Park data (such as occurred in our and Stenlund's samples) would tend to obscure the preponderance of males in the adult sample.

The adult subsample of hunter-kills also contained a higher percentage of males (66 percent : 34 percent). Although this might also reflect the influence of wolf predation on female fawns, it probably is more a result of the greater movement of bucks during the hunting season, which overlaps with the rutting season. Even the sex ratio of adult deer killed in wolf-free areas shows a preponderance of males (Erickson *et al.* 1961).

However, it appears that the higher harvest of bucks by human hunters does markedly affect the sex ratio of the deer population in the hunted area, for the wolf-kill of adults in that area contained a significantly higher percentage of does (56 percent) than did the wolf-kill of adults in the wilderness area (29 percent).

Evidently the hunter harvest is not heavy enough to affect the age structure of the deer population to any marked degree, for no significant difference in age structure was found between the wolf-kill in the hunted area and that in the wilderness area (table 1). This does not conflict with the conclusion that hunting affects the sex ratio of the deer herd, because it would take much less to influence a population characteristic having two classes (sex) than one having 14 (age).

One additional difference in the sex ratio was found between two other subsamples of the wolf-kill – that is, the wolf-kill before and after an unusually high snow accumulation, which reached its peak about February 1, 1969 (table 1). Of a total of 77 animals killed before this snow condition occurred (including those from previous years), 38 percent were females. Of 44 animals killed after the heavy accumulation, 57 percent were females. One possible explanation for this is that females may normally be less vulnerable to wolf predation, for Kelsall (1969) has shown that they probably have a lighter weight-load-on-track than males. Thus when snow conditions changed greatly, making deer generally much more vulnerable to wolves (see Mech *et al.*, p. 35), a preponderance of does suddenly might have become available. There is some evidence that does may be generally less vulnerable under most conditions, for all seven of our wolf-killed deer over 10 years old were females, and the oldest was over 14.

Condition of Wolf-Killed Deer

Because the data show that wolves in our study area tend to kill a disproportionate number of older deer, it is not surprising to discover that wolves also tend to capture a disproportionate number of individuals with abnormalities and pathological conditions (table 8). The explanation for such selection is obvious in regard to the abnormalities of the lower limbs (figs. 14-17): deer with injured or abnormal limbs simply cannot run as fast or as agilely as normal animals (table 7). Our observations show that deer usually depend on their alertness and speed to escape approaching wolves (Mech 1966b, Mech *et al.*, p. 1). Any trait or condition that tended to interfere with either alertness or speed would decrease an individual's chance of escape.

It is more difficult to explain how dental abnormalities or pathological conditions of the mandible (figs. 8-10) would predispose an individual to wolf predation. However, in the case of dental abnormalities the genetic or environmental conditions that caused the abnormality might also have caused some other trait that increased the animal's vulnerability. Or the abnormal condition itself may have caused a further, more critical, disruption of the animal's physiology or behavior, which in turn predisposed it to wolf predation.

The finding of several wolf-kills with poor fat stores could indicate that primary or secondary malnutrition was a factor in the animals' deaths. However, it would take a statistical comparison between the fat stores of the deer at large and those of the wolf-kills to establish this.

The discovery that 13 percent of the fawns and 84 percent of the yearlings killed during January, February, and March had not yet shed their deciduous incisors and premolars, respectively, also fits well with the rest of our information. Evidently some unusual factor had caused the delay in tooth development and replacement. One possibility is that the animals were born in August or September, much later than normal. Although most deer in Minnesota are born in May and June, there are records of births in July and August. In addition, a fetus 181 to 200 days old was found in a doe killed on September 26 (Erickson *et al.* 1961).

An alternate explanation for the delay in tooth replacement is that the animals were suffering from malnutrition or nutrient deficiency. Severinghaus[2] has evidence that yearling bucks that have not replaced their deciduous premolars during November, and thus are aged at 17 months (Severinghaus 1949), generally have shorter, narrower antlers and fewer points than 18- and 19-month-old individuals. Degree of antler development in turn is considered related to nutritional state (Latham 1950). Thus it is reasonable to conclude that animals behind in tooth development and replacement, whether this is caused by age or diet, are physiologically inferior.

Most of the abnormal conditions discussed above pertain to the skeletal parts of wolf-kills. If the soft parts of a large number of kills could be examined thoroughly, one might discover a much higher incidence of diseases and other pathological conditions.

In conclusion, our data on both age and condition of wolf-killed deer show that at least during winter, wolves in our study area usually do not kill just any deer they discover, although they do try to. Evidently, most deer can usually escape wolf predation. The most frequent exceptions are those 5½ years old and older, those born late, those suffering from poor nutrition, those with abnormalities or pathological conditions, and possibly fawns.

The above conclusions parallel those of Murie (1944), Crisler (1956), Mech (1966a), and Pimlott *et al.* (1969) for wolves preying on Dall sheep, caribou, moose, and deer respectively, and further substantiate the claim by Mech (1970) that they can be extended to wolves preying on most, if not all, species of large mammals under most conditions. It is also apparent from the data presented above that deer over 5 years of age and those with abnormalities of the jaw or lower limbs represent such a small percentage of the total population that they are seldom taken by human hunters. In this respect, competition between timber wolves and human hunters appears to be minimal in the study area.

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[2] *C. W. Severinghaus. Unpublished data.*

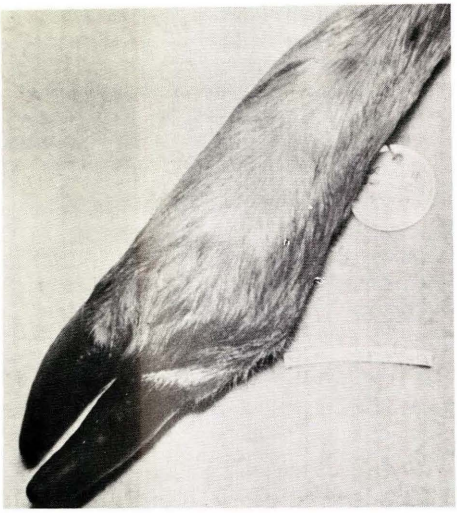

Figure 14.—Arthritis in right hind foot of specimen M-28. (Photo courtesy of University of Minnesota Veterinary Diagnostic Laboratory.)

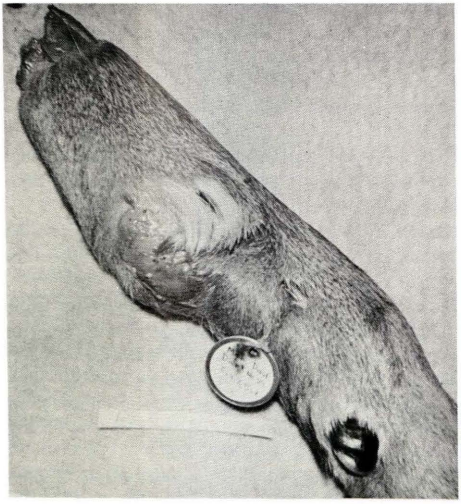

Figure 15.—Infection and fibrous mass in a front foot of specimen M-29. (Photo courtesy of University of Minnesota Veterinary Diagnostic Laboratory.)

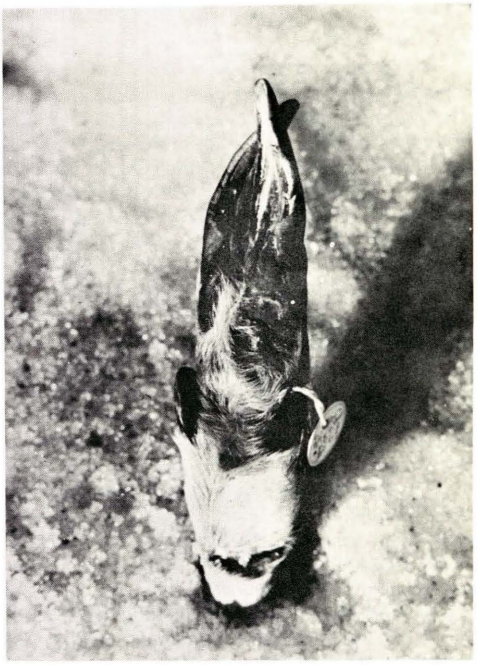

Figure 16.—Injury to left front foot of specimen M-196. (Photo courtesy of L. D. Mech).

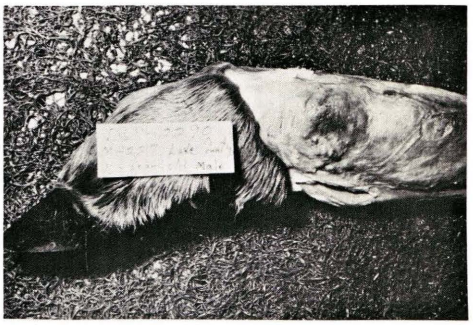

Figure 17.—Healed fracture of left hind leg of specimen M-227. (Photo courtesy of University of Minnesota Veterinary Diagnostic Laboratory.)

SUMMARY

White-tailed deer (*Odocoileus virginianus*) killed by wolves (*Canis lupus*) during winter in a relatively unhunted wilderness area and in an immediately adjacent hunted area of Minnesota were compared with deer killed by hunters in the same general area, and with a hypothetical population. Deer killed by wolves were significantly older. Statistical comparisons also showed the following: (1) hunters generally killed an even sex ratio of fawns, and a disproportionate number of adult bucks, (2) wolves took a higher percentage of female fawns than female adults, a disproportionate number of bucks in the wilderness area, and a higher percentage of does in the hunted area. The latter fact evidently reflects the higher hunter success on males in the hunted area. Significantly higher incidences of abnormalities and pathological conditions of both mandibles and lower limbs were found in wolf-killed deer than in hunter-killed deer, and these conditions are described. It is concluded that wolf predation on white-tailed deer in the study area during winter generally is selective in that it tends to remove members of the prey population that are old, debilitated, or abnormal. Apparently these classes of deer represent such a small percentage of the population that they are seldom taken by human hunters.

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Mr. David W. Kuehn sectioned the incisors of the deer jaws and determined their ages. Dr. Donald M. Barnes of the University of Minnesota Veterinary Diagnostic Laboratory examined the abnormal lower limbs, described their pathology, and provided photos of specimens used herein.

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The following individuals read the manuscript and offered many helpful suggestions: Mr. R. L. Downing, Mr. C. W. Severinghaus, Mr. J. M. Peek, Dr. C. T. Cushwa, Mr. M. H. Stenlund, and Dr. R. R. Ream.

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THE EFFECT OF SNOW CONDITIONS ON THE VULNERABILITY OF WHITE-TAILED DEER TO WOLF PREDATION

L. David Mech, L. D. Frenzel, Jr., and P. D. Karns

Wolves (*Canis lupus*) and deer (*Odocoileus virginianus*) having evolved together, no doubt have become adapted to contending with each other's physical abilities. Thus it is not surprising to learn that deer which succumb to wolf predation are generally weaker, older, or abnormal compared with the total deer population (Pimlott *et al.* 1969, also see Mech and Frenzel, p. 35).

However, the structural and behavioral adaptations of both species must have evolved under environmental conditions that are average or usual; otherwise, an adjustment of wolf to deer populations, and vice versa, could not have been maintained over long periods. This implies that extreme or unusual conditions might sometimes occur, to which either the wolf or the deer is poorly adapted.

One of the most important environmental factors that can influence the interactions of wolves and deer is snow. The total fall, depth on the ground, and the density are all aspects of snow that may vary considerably and affect the ability of wolves to capture deer. Recent studies of wolves and deer in northeastern Minnesota (see Mech *et al.*, p. 1, also Mech and Frenzel, p. 35) afforded us opportunities to investigate the relationships between snow and the interactions of wolves and deer.

METHODS

Two principal methods of study were used in this investigation. The first involved recording the snow depth and support quality ("penetrability") in feet and tenths of feet (Verme 1968). Snow measurements were taken during the winters of 1966-67, 1967-68, and 1968-69, in which large differences in snow conditions existed. Ten such measurements were made weekly near Isabella, Minnesota, in an open aspen (*Populus tremuloides*) stand away from influences that might have caused drifting or other unusual snow conditions; the measurements were averaged.

Penetrability was determined with Verme's snow-compaction gauge – a 3-foot piece of 1⅛-inch (outside diameter) copper tube filled with lead to total 3 pounds, which gives a weight per area of 211 gm./cm.^{2}. To obtain a measurement, the pipe is held vertically with its lower end just flush with the snow, and then is released. The depth to which it sinks is considered the penetrability of the snowpack by a walking deer.

Although the snow conditions measured at Isabella are not representative of the entire study area, year-to-year comparison in the Isabella area should also apply generally throughout the region.

The second technique used in this study was observing the movements of wolves and deer. This was usually done from low-flying aircraft, and was facilitated by the use of radiotracking, as described by Mech *et al* (p. 1). Close inspection of wolf-killed deer was made from the ground (Mech and Frenzel, p. 35).

RESULTS AND OBSERVATIONS

Snow measurements for each winter are shown in figures 1 through 3. The winter of 1968-69 was the most extreme of the three in terms of accumulated snow, and was generally regarded as having one of the heaviest snowfalls and accumulations on record for the study area. Snow depth on the level near Isabella reached 3.9 feet at one time, and from January 3 to April 4 it exceeded 2.4 feet. The highest snow level reached during 1966-67 was 2.4 feet, and the highest level reached during 1967-68 was 1.4 feet. In the vicinity of Ely, some 30 miles from Isabella, the 1968-69 peak accumulation was 39 inches, the highest accumulation since 1948-49 when records were first kept.[1] Thus we consider the winters of 1966-67 and 1967-68 to be within the normal range for the study area, and the 1968-69 winter as being most unusual (fig. 4).

The snow penetrability in 1966-67 remained high throughout January, February, and March. During the following winter, penetrability fluctuated more, but even at its greatest, it was relatively unimportant to deer because the total

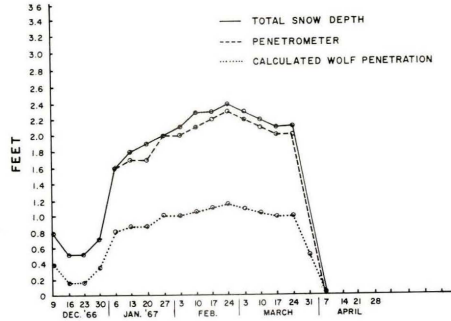

Figure 1.—Snow depth and penetrability by deer and wolves near Isabella, Minnesota, 1966-67.

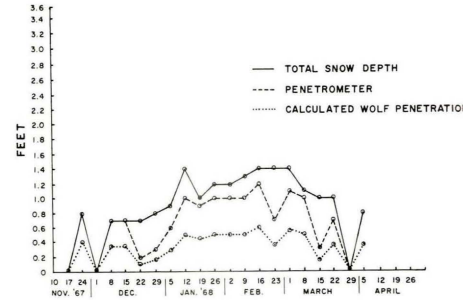

Figure 2.—Snow depth and penetrability by deer and wolves near Isabella, Minnesota, 1967-68.

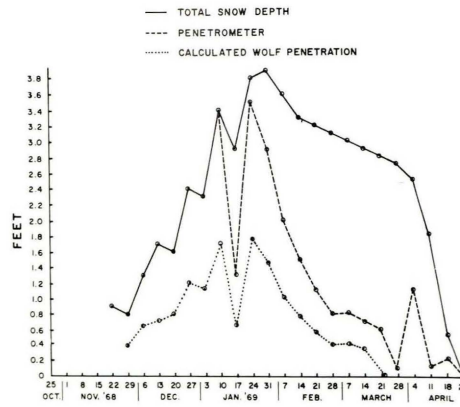

Figure 3.—Snow depth and penetrability by deer and wolves near Isabella, Minnesota, 1968-69.

[1] *M. H. Stenlund. Personal correspondence to to L. D. Mech, Oct. 10, 1969.*

Figure 4.—During the winter of 1968-69, the snow was unusually deep in the study area. (Photo courtesy of L. D. Frenzel.)

snow depth was so low. During 1968-69, however, penetrability was a very important aspect of snow condition. It was so high during late January and early February, when snow accumulation was also at its peak, that a walking deer would be expected to sink in 2.5 to 3.5 feet. Snow penetrability then decreased through February and March to a point where a walking deer would sink in approximately 0.6 foot on March 21. However, because snow accumulation remained so high through February and March, the lower penetrability during late February and March still afforded no relief to running deer, because they must exert forces several times as great as when walking. On the contrary, the low penetrability (which is an indirect measure of density) could be expected to hinder a running deer in deep snow, for it would cause much more resistance.

Deer movements, like snow conditions, varied greatly during the three winters of the study. During the first two winters, deer were generally found singly and in groups of two to six, often around the shores of lakes but also scattered about inland. In late January and February 1967, running deer were observed sinking deeply into snow, but their movements still did not seem to be hindered, no doubt because of the high penetrability (low density) of the snow that year (fig. 1).

However, during late January, February, and March of 1969 the deer were much more concentrated, mostly in conifer swamps, along southwest-facing slopes, or on lakes. Although groups of two or three animals could be found in scattered inland "pockets" throughout the winter, groups of five or six were not uncommon on lakes during January. The tendency to concentrate continued to increase, and on February 6, as many as 11 deer were observed on one lake; by March 13, group size had increased to as high as 22 deer in the same area. Throughout February and March, heavy concentrations of deer tracks covered most wilderness lakes, further evidencing much greater use of shorelines than had occurred in the two previous winters (fig. 5).

No doubt deer tended to concentrate on lakes because travel inland became so difficult. On January 28, two deer were seen plowing through snow up to their necks. Although the snow began settling in February, and the penetrability decreased, by late February running deer still plunged chest-deep and had to hesitate at every bound. These conditions persisted until about March 26, by which time a surface crust strong enough to hold a running deer had formed.

Figure 5.—Under unusually deep snow conditions, deer used lake shores heavily. (Photo courtesy of L. D. Mech.)

In considering wolf mobility in snow, two types of movement must be recognized: the trot used during general travel, and the bounding used while chasing prey. The trot is an easy gait of about 5 m.p.h. on firm footing (Mech 1970), and can be continued for hours at a time. During periods of deep snow and high penetrability, most wolf travel is on frozen waterways, roads, snowmobile trails, and animal trails, including the wolves' own pathways, which become well packed with frequent use (fig. 6, 7A, B). Such travel was observed during each of the three winters of this study.

The second type of wolf movement affected

Figure 6.—Wolves travel single file in deep snow. (Photo courtesy of L. D. Mech.)

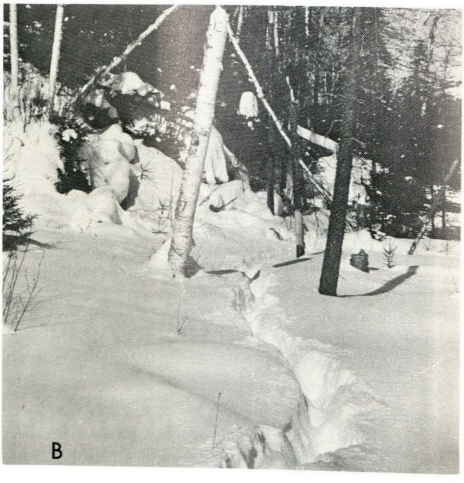

Figure 7.—(A) A single wolf must break his own trail through the snow. (Photo courtesy of L. D. Frenzel.) (B) Regular use by a pack keeps trails open. (Photo courtesy of L. D. Mech.)

by snow is the leaping and bounding associated with chasing prey. The shallower angle of the wolf's bound (fig. 8) (compared with that of the deer) often causes the wolf to flounder in snow that presents little hinderance to deer (Mech 1970). Such was the case in January and February 1967 in our study area. During 1967-68 no observations of wolves chasing deer were made by the authors, but reports by other field workers indicated that running conditions were similar to those of 1967.

During the winter of 1968-69, wolves also bogged down a great deal in snow when chasing deer. However, after January 1969 the snow was so deep that deer were floundering even more than wolves in many cases. The fact that wolves could run in the trail broken by deer probably also gave the wolves an advantage under the conditions that severely restricted deer movements.

The above observations of snow conditions, deer movements, and wolf movements during the three winters of the study are in accord with observations made on the differences in the ability of the wolves to capture deer during the same period. Two indices support the conclusion that wolves had a much easier time catching deer during February and March 1969 than earlier in the winter and in the two previous winters: (1) the degree of utilization of wolf-killed deer, and (2) the kill rate of radiotagged wolves.

During the winters of 1966-67 and 1967-68, and in December and early January1968-69, most wolf-killed deer found had been thoroughly eaten, and the bones – if present at all – were well chewed and scattered at each kill (fig. 9). All skin and flesh from the skull were eaten, and the mandible was usually separated from the skull. During late February and early March 1967, few fresh kills were even found, and wolves were returning several times to old kills that had been cleaned up many days before.

However, in late January 1969 a substantial change began taking place. The skeletons of most kills found were almost intact, the flesh having been eaten from around the bones (fig. 10). Appreciably more skin was usually left on the carcass, especially on the side lying on the snow, and the neck and head were generally intact. This was true even of fawns, which in the past often were almost completely consumed.

In several cases, only about half of the flesh had been eaten from the carcasses. On February 2, 1969, four deer recently killed by wolves were found along a 1½-mile stretch of Birch Lake

Figure 8.—Wolves run at a shallow angle, thus hindering them in deep snow. (Photo courtesy of D. H. Pimlott.)

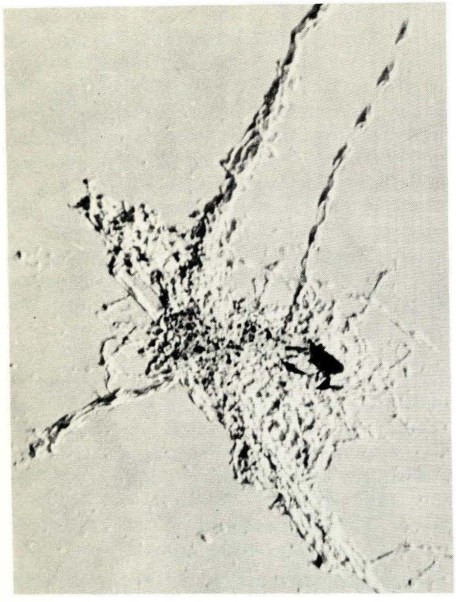

Figure 9.—Usually the remains of a wolf kill are well chewed and scattered before the wolves abandon them. (Photo courtesy of L. D. Mech.)

Figure 10.—During a period of especially deep snow, wolves abandoned many kills before pulling apart the skeletons. (Photo courtesy of L. D. Mech.)

and nearby Polaris Lake (Minnesota-Ontario border). One large doe was completely uneaten and remained so for at least 24 hours after discovery from the air. Further, one fawn had only a few pounds of flesh eaten, a yearling doe was half eaten, and another fawn was about 75 percent eaten. Hazardous landing conditions during this period severely limited the number of carcasses that could be examined from the ground, but on February 6 a yearling doe was discovered that had only about 5 to 10 pounds of flesh eaten, and on February 8 an adult doe was found that was completely intact except for wounds.

In past winters some kills had been located that had been only partly eaten, but in each case the carcasses were soon revisited and cleaned up (Mech 1970). This was often not the case in 1969. For the rest of the winter most of the deer killed by wolves in our study area were not as completely consumed as in previous winters. Pimlott *et al.* (1969) found a similar relationship between the severity of the winter and the degree to which wolf-killed deer were utilized.

Correlated with the above information was the kill history of our radiotagged wolves (Mech *et al.*, p. 1). From December 1968 through January 1969 No. 1051 had killed three or possibly four deer, and generally had spent 6 or 7 days feeding on each. However, throughout most of February this animal visited a new deer carcass (which presumably he killed) every 3 days, and he spent only 1 or 2 days at each. In two cases two new carcasses were found in the immediate vicinity of this animal during the same day, and in each case the wolf spent only 1 day in the area. A second wolf (1053) which had spent most of December and January scavenging on the remains of both deer and moose (*Alces alces*) that had died long before, made her first known kill of a deer on January 31, 1969. The kill rate of the other three radiotagged wolves also increased, although the data for them are less com-

plete. The average kill rate for all radiotagged wolves and their associates was one deer per wolf per 16 to 20 days before February 1, and one per 8 to 12 days after February 1 (see Mech *et al.*, p. 1).

DISCUSSION AND CONCLUSIONS

Under usual snow conditions throughout most of the range of the white-tailed deer, healthy vigorous individuals can probably escape most attacks by wolves. Observations by Mech (1966), Rutter and Pimlott (1968), and Mech *et al* (p. 1) indicate that a high percentage of attempts by wolves to kill deer during winter are unsuccessful. This is further implied by the figures of Pimlott *et al.* (1969) and Mech and Frenzel (p. 35) showing that at least during winter wolves tend to kill a disproportionate number of old deer as well as those with various abnormalities and pathological conditions.

However, during a winter with extremely deep snow, the usual relationships seem to change somewhat. Fewer deer are able to escape wolves, and a surplus is killed. This means that some individuals not vulnerable under the usual snow conditions become vulnerable during extreme conditions. There are two main possible reasons for this, the effect of the extreme weather conditions on the health and vigor of the deer, and the physical effect of the snow on the escapability of the deer.

In regard to the first possibility, there was limited evidence that during February and March 1969 some fawns and yearlings in our study area were losing their fat stores. Two of three yearlings, and both fawns intact enough for examination during this period lacked back fat, and the marrow in one of six fawn femurs was partly fat depleted. Nevertheless, the third yearling inspected still had back fat, and a 3½-year-old doe had heavy omental, renal, heart, and back fat during the same period. Thus, although an abnormal decline in the physical condition of some deer in the late winter might partly account for the increased kill by wolves during February and March 1969, the effect of snow on the escapability of the deer probably was also involved.

The key difference in snow conditions between the two periods – (1) the winters of 1966-67, 1967-68, and December-January 1968-69, and (2) February and March 1969 – was the heavy, persisting accumulation of snow during the latter period, combined with the increasing density of the snow. As our observations show, this greatly hindered the movements of deer fleeing from wolves.

Under more usual conditions, a running deer might sink through the snow to the ground and thus obtain a firm footing from which to spring again. In discussing wolf-caribou relations in snow, Kelsall (1968, p. 249) stated the following: "While caribou (*Rangifer tarandus*) will sink into snow even deeper than wolves, their longer legs permit them to run efficiently where a wolf will bog down. Nasimovich (1955) considered that roe deer and sika deer could be taken by wolves when snow was not more than 30 cm. (11.8 inches) in depth. At depths above that their pursuit becomes difficult or fruitless."

However, it appears that when snow becomes extremely deep, wolves then gain the advantage. With 22 to 48 inches or more of snow to plow through, a deer would have trouble even touching a firm foundation. According to Kelsall (1969), deer measure only 20 to 24 inches from hoof tip to chest, with legs extended.

It is true that wolves stand even shorter than deer and so might be expected to flounder even more. However, this is where another factor becomes important, the "weight-load-on-track" or total weight per area of track. As Kelsall (1969) has pointed out, the mean weight-load-on-track for deer is extremely difficult to measure directly, because the actual under-surface of the deer's foot slants vertically, and a much greater area may be used to support an animal in snow than on a hard surface. This probably explains the discrepancy between Kelsall's measurements and work done by Verme (1968) in Michigan. According to Kelsall, deer weight-load-on-track (hoof only) varies between 431 and 1,124 gm/cm.^{2}. However, Verme stated that his compaction gauge (with a weight load of about 211 gm./cm.^{2}, described earlier in this paper) sank in virtually the same amount in snow as did deer. Under the snow conditions in our study area, we found that the same type of compaction gauge generally penetrated to a depth within a half inch of that to which deer were sinking. On this basis, it seems reasonable to suggest that a deer in snow is supported by more of its foot than

just the hoof, and that the actual weight-load-on-track of deer in snow is about 211 gm./cm.^{2}.

For wolves, this measure varies from 89 to 103 gm./cm.^{2} (Foromozov 1946). This means that for the same amount of force applied during running, a wolf would have twice as much support as a deer. It also means that in deep snow a walking wolf generally is much less restricted than a walking deer. Late in February 1969, for example, when deer were seriously limited in their ability to travel, wolves were able to travel widely (Mech *et al.*, p. 1).

Even though wolves have much greater support than deer, when running they still sink into the snow almost as much as deer under most conditions, probably because both run with such force that snow usually offers little support. Nevertheless, with extremely deep snow, the difference in support factor between wolves and deer could become critical, and this is probably what happened during February and March 1969. With deer seriously restrained by the deep snow, even a slight advantage in favor of the wolf could increase hunting success. A high snow density during that period would accentuate this advantage. This is because until the snow becomes dense enough to hold a running deer, each increase in density would further the advantage of the wolf, which would require only half the density to support it, while it would hinder the deer.

One result of the extreme snow conditions of early 1969 was that deer tended to gravitate to lakes, where snow was shallow and footing was firm. Initially upon disturbance by human beings, and probably by wolves, these deer usually headed inland, but it is apparent from a number of kills examined that when pressed hard by wolves inland, deer headed out onto lakes where possible. Apparently they could run there with better footing. However, frozen lakes also provide wolves with good running conditions, and even seem to give them an advantage (Rutter and Pimlott 1968, Mech 1970), so many of these deer were killed (fig. 11).

Stenlund (1955, p. 44) reported as follows on years of low snowfall, the opposite condition, which demonstrated the same relationship between snow depth and kills on lakes: "The winters of 1951-52 and 1952-53 were abnormally mild with little early snow. As a result, few

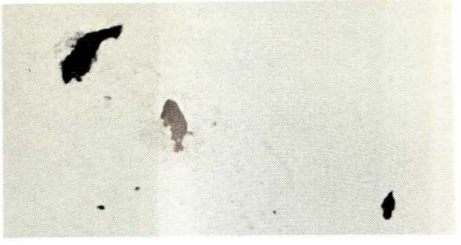

Figure 11.—On frozen lakes, wolves often seem to have the advantage over deer, such as in this case where the wolf (center) has just killed a deer and is trying to discourage a raven from joining him in the feed. (Photo courtesy of L. D. Frenzel.)

wolf-killed deer appeared on the lakes and most deer attempted to outrun wolves in the woods."

Thus it appears that extreme snow conditions in our study area increase the vulnerability of deer to wolf predation in three ways: (1) by causing a decline in the health and nutritional state of some members of the deer population; (2) by hindering the escapability of the deer; and (3) by causing deer to congregate on frozen lakes where wolves have the advantage in running.

SUMMARY

During the winters of 1966-67, 1967-68, and 1968-69, the interactions of wolves (*Canis lupus*) and white-tailed deer (*Odocoileus virginianus*) were observed in northeastern Minnesota from aircraft. Snow depth and supporting ability were also measured during these winters, and the ability of wolves to capture deer was compared for a period of usual snow conditions versus a period of extreme snow conditions.

It was found that during February and March 1969, when snow remained from 2.5 to 3.9 feet deep and failed to support running deer, wolves were able to capture deer more easily. This was evidenced by kills that were left partly or completely uneaten, and by a higher rate of predation by radiotagged wolves and their associates.

Although both wolves and deer floundered in the extremely deep snow, the relatively lighter weight-load-on-track of wolves evidently gave

them a greater advan than under the usual snow conditions, wh wolves were observed floundering more tha er. This factor, plus a decline in the health vigor of some segments of the deer populati d a tendency for deer to congregate on froz akes, where wolves have an advantage, help e n the increased vulnerability of deer to predation during the winters of deep snow.

ACKNOWLEDGMENTS

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THE POSSIBLE OCCURRENCE OF THE GREAT PLAINS WOLF IN NORTHEASTERN MINNESOTA

L. David Mech and L. D. Frenzel, Jr.

The timber wolf (*Canis lupus*) of northeastern Minnesota occupies an area within the range given by Goldman (1944) for the eastern timber wolf (*C. l. lycaon* Schreber). However, this area is within 150 miles of the eastern edge of the former range of the Great Plains wolf (*C. l. nubilus* Say), and there is some question as to whether the Minnesota wolf is really an intergrade between these two subspecies. Writing of *nubilus*, Goldman (1944, p. 444) stated: "Specimens from eastern Minnesota and Michigan seem more properly referable to *lycaon*, but relationship to *nubilus* is shown in somewhat intermediate characters."

In describing *lycaon* as basically a gray wolf, Goldman made no mention of the occurrence of black or white color phases in that subspecies. However, in discussing *nubilus*, Goldman (1944, p. 442) wrote the following: "Many color variations are presented. Individuals may be nearly white at any season, except for a sprinkling of black hairs over the back, a small, narrow, but conspicuous, black patch over the tail gland, and a more or less distinctly black tip. Black individuals may occur in the same litter with those normally colored." Goldman also referred to *nubilus* as "now probably extinct."

In the eastern part of the range of *lycaon*, color phases other than gray appear to be rare as Rutter and Pimlott (1969, p. 188) attest: "The uniformity of the color of timber wolves in many areas is evidenced by the work in Algonquin Park, in Ontario. There, over the past eight years, dozens of packs have been observed from the air. However, we have never been able to discriminate between any of them on the basis of the color variation of individual animals."

Thus it seems significant to report on incidences of black and white color phases in wolves that we have observed in northeastern Minnesota during some 480 hours of flying associated with wolf research (Mech *et al.*, p. 1). The observations took place in the Superior National Forest, in northern Cook, Lake, and St. Louis Counties during the winters of 1966-67, 1967-68, and 1968-69. A total of 309 sightings were made of wolves that could be classified by color; of these, 11 (3.6 percent) were jet black (fig. 1) and two (0.6 percent) were creamish white, with the cream color the most intense on the back. No doubt some of the grays, and perhaps the blacks and whites, were repeated observations, but the figures should provide a reasonable approximation of the incidence of these color phases in this area. All black or white animals except one were observed with gray wolves (table 1 and fig. 2).

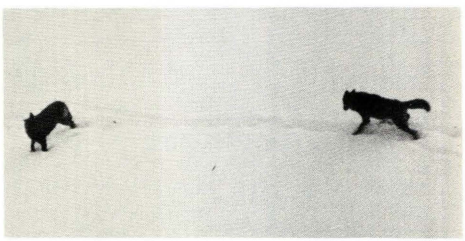

Figure 1.—A few wolves observed in the study area were jet black. (Photo courtesy of L. D. Mech.)

A number of black wolves, and a few white wolves, have been seen by other observers, all in the three counties listed earlier. To gain some idea of the past incidence of these color phases in the same general area, we asked Conservation Officers Robert Hodge, Robert Jacobsen, and Frank Baltich of the Ely, Minnesota, area about the numbers of each phase that they took before 1960. They reported killing an approximate total of 580 wolves, of which four were black and three were white or creamish white.

Because black and white color phases have rarely if ever been reported for *lycaon*, yet were

Table 1.—Observations of wolves of black and white color phases

Date	Location		Color combinations within each pack
Feb. 24, 1967	T64N-R8W-S1	Vera Lake	3 grays; 1 black; 1 white
Mar. 4, 1967	T63N-R9W-S27	Lake Two	3 grays; 2 blacks
Dec. 18, 1968	T63N-R8W-S35	Lake Insula	2 grays; 2 blacks[1/]
Jan. 17, 1969	T65N-R8W-S27	Carp Lake	1 gray; 1 white
Feb. 1, 1969	T63N-R8W-S13	Lake Insula	4 blacks; 2 grays[2/]
Feb. 5, 1969	T63N-R8W-S8	Benezie Lake	1 black
Feb. 6, 1969	T63N-R10W-S33	Clear Lake	3 grays; 1 black

1/ These animals were near the shore of the lake, so others may have been inland where they could not be seen.

2/ This group might well have been the same as that seen on Dec. 18, 1968.

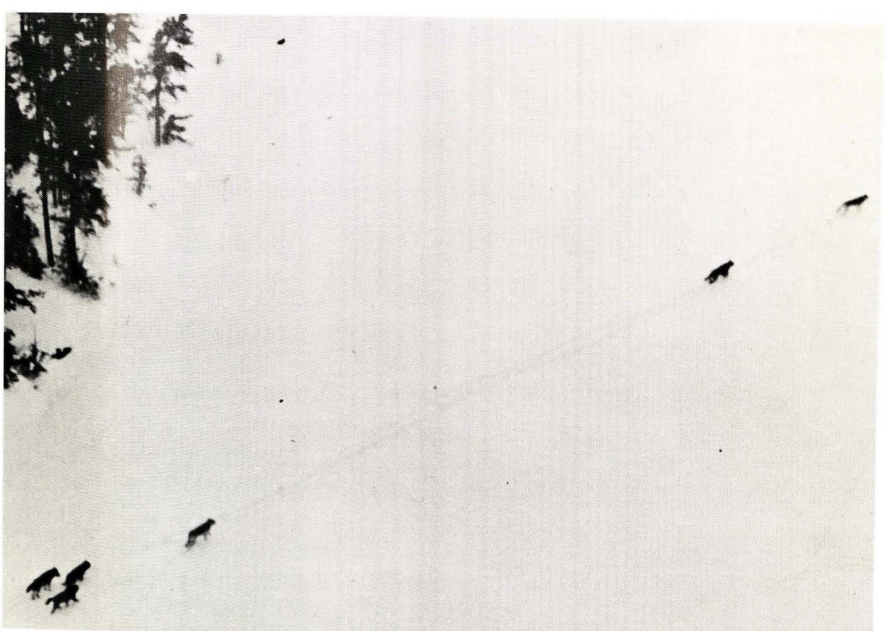

Figure 2.—A pack of four blacks with two grays (first and third). (Photo courtesy of John Winship.)

well known for *nubilus*, it is not unreasonable to conclude that the race of wolves now occupying northeastern Minnesota does show strong *nubilus* influence. Goldman examined the skulls only of 10 Minnesota specimens assignable to *lycaon* and only one referable to *nubilus*. Because wolves in the known range of *nubilus* are thought to be extinct, and because the animals in northeastern Minnesota are legally unprotected and subject to a control program, it seems highly desirable that the question of their taxonomy be studied intensively while specimens are still available.

ACKNOWLEDGMENTS

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